MAGDALENA BORSUK-BIAŁYNICKA

ANGUIMORPHANS AND RELATED LIZARDS FROM THE LATE CRETACEOUS OF THE GOBI DESERT, MONGOLIA

(Plates 1—13)

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Lizards of the infraorder Anguimorpha (superfamily Platynota) and related forms are described on the basis of Late Cretaceous skull material from the Gobi Desert. The material comes from Barun Goyot Formation of ?middle Campanian age and its equivalents and from Djadochta Formation of ?late Santonian and/or ?early Campanian age. Five new genera and species of Platynota are described. *Proplatynotia longirostrata* and *Gobiderma pulchra* are provisionally left without familial assignment. *Parviderma inexacta*, *Cherminotus longifrons* and *Saniwides mongoliensis* are assigned to Necrosauridae, Lanthanotidae and Varanidae respectively, *Cherminotus* being the only fossil representative of the family. New osteological data of *Telmasaurus grangeri* GILMORE, 1943 (Platynota) are given. Two new genera and species, *Bainguis parvus* and *Paravaranus angustifrons* are probably related to Anguimorpha and are assigned to two new families Paravaranidae and Bainguidae, superfamily and infraorder uncertain. The relationships are analyzed with the help of the cladistic techniques of Hennig. An attempt is made to ascertain the polarities of characters. Skull kinesis is discussed on the basis of FRAZZETTA's (1962) model. Depression of the snout below the resting position, referred to as overretraction is considered critical to the development of a saurian type of kinetic activity. A model is proposed in which loss of the pterygovomerine contact, formation of a sliding pterygopalatine joint and loss of quadratojugal are structural changes that act to reduce horizontal stress. It is assumed that this stress is generated by overretraction within a skull floor lacking an hypokinetic axis. The evolution of the studied part of the autarchoglossan stem is conceived in gradal terms, preanguimorphan, necrosaurian and modern platynotan morphological grades being recognized.

Key words: Lizards, Anguimorpha, Platynota, Upper Cretaceous, Mongolia, cranial morphology, cranial kinesis.

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ANGUIMORPHA I POKREWNE IM JASZCZURKI Z GÓRNEJ KREDY PUSTYNI GOBI, MONGOLIA

Streszczenie. — Praca zawiera opis jaszczurek należących do Anguimorpha (6 gatunków) lub pokrewnych tej grupie (2 gatunki) pochodzących z górnokredowych osadów pustyni Gobi (z Formacji Dżadochta — ?g. santon lub/i ?d. kampan oraz z formacji Barun Gojot i jej stratygraficznych ekwiwalentów datowanych na ?śr. kampan, patrz GRADZIŃSKI

i in. 1977). Materiał pochodzi ze zbiorów polsko-mongolskich wypraw na pustynię Gobi z lat 1963—71 i obejmuje ok. 20 okazów, w przeważającej części czaszek, na których też oparte zostało niniejsze opracowanie; nieliczne i słabo zachowane fragmenty szkieletu pozaczaszkowego zostaną opracowane później.

Spośród pięciu monotypowych rodzajów z gatunkami: *Proplatynotia longirostrata*, *Gobiderma pulchra*, *Parviderma inexacta*, *Cherminotus longifrons* i *Saniwides mongoliensis* dwa pierwsze zaliczone zostały do nadrodziny Platynota bez przynależności rodzinowej, pozostałe zaś odpowiednio do Necrosauridae, Lanthanotidae i Varanidae, z których Lanthanotidae nie były dotąd znane w stanie kopalnym. Praca zawiera nowe dane osteologiczne na temat gatunku *Telmasaurus grangeri* GILMORE, 1943 (Varanidae). Oparte są one na nowym materiale pochodzącym z osadów formacji Barun Gojot datowanych na ?śr. kampan, a więc młodszych of Formacji Dżadochta (?g. santon lub/i ?d. kampan), z której pochodził holotyp. Dwa następne monotypowe rodzaje z gatunkami *Bainguis parvus* i *Paravaranus angustifrons* to formy mozaikowe łączące pewne cechy Anguimorpha z ogólnie prymitywną budową i na tej podstawie są prowizorycznie łączone z Anguimorpha. Zostały one zaliczone do dwóch nowych rodzin Bainguidae i Paravaranidae (superfamilia *incerta*). W opisanym materiale brak przedstawicieli nadrodziny Diploglossa, której obecność w g. kredzie Azji nie została dotąd stwierdzona.

Pod względem metodologicznym praca oparta jest na zasadach kladyzmu (HENNIG 1966, SCHAEFFER i in. 1972, HECHT 1976). Hipotezy dotyczące pokrewieństw formułowano w postaci rozkładów cech uznanych za pochodne (derived) w oparciu o kryteria morfologiczne. Zastosowano typowe dla kladyzmu graficzne przedstawienie hipotez w postaci kladogramów, na które, dla jasności obrazu, naniesiono numerowane punkty oznaczające stany cech. Dla uzupełnienia obrazu na kladogramach uwidoczniono też rozkład stanów plezjomorficznych.

Część ogólna pracy zawiera omówienie poszczególnych cech kraniologicznych, zmierzające do sprecyzowania (1) zakresu ich zmienności w obrębie taksonów poniżej szczebla podrzędu, (2) cech rozwoju osobniczego, wskazania (3) wzajemnej korelacji pewnych cech oraz (4) ustalenia następstwa stanów cech (morphocline polarity). Ta część pracy zawiera dyskusję zjawiska kinetyzmu czaszkowego opartą na modelu FRAZZETTY (1962), oraz interpretację kierunku rozwoju cech pokrycia osteodermalnego czaszki oraz cech puszki mózgowej w filogenezie. W części dotyczącej kinetyzmu podkreślono szczególną rolę opuszczania części przedoczodołowej czaszki (snout unit) poniżej pozycji spoczynkowej w czasie działania mechanizmu czaszkowego. Pozycja ta, nazwana tu nadretrakcją (over-retraction) jest cechą charakterystyczną typu przystosowawczego Sauria, z którą przypuszczalnie związane są podstawowe cechy strukturalne czaszki jaszczurek. U większości jaszczurek z opisanego materiału występuje charakterystyczny, skośny i przypuszczalnie mający możliwość suwu, staw skrzydłowopodniebienny. W pracy zaproponowano model, w którym powstanie takiego stawu, utrata kontaktu skrzydłowo-lemieszowego i zanik kości kwadratowo-jarzmowej byłyby odpowiedzią na napięcie działające poziomo spowodowane przez nadretrakcję mechanizmu czaszkowego przy pierwotnym braku stawu hypokinetycznego.

Rozważania na temat pokrycia osteodermalnego czaszki oparte są na znanym fakcie współzależności między składnikiem mezodermalnym i epidermalnym szkieletu skórnego. Przypuszcza się, że postać pokrycia epidermalnego jest uzależniona od postaci leżących pod nim kości, tam, gdzie skóra ściśle do nich przylega. Z kolei postać elementów osteodermalnych zależy od postaci elementów epidermalnych. Słabe przyleganie skóry do kości lub ich brak w bezpośrednim sąsiedztwie skóry powoduje tworzenie pokrycia skórnego w postaci małych elementów rosnących obwodowo z tendencją do tworzenia struktury typu plastra miodu (tesselated pattern). Na podstawie badania wczesnych stadiów rozwojowych pokrycia osteodermalnego oraz rozkładu tej cechy w grupach zewnętrznych (outgroups) w stosunku do Anguimorpha stwierdzono, że prymitywnym stanem tego pokrycia jest inkrustacja kości czaszki substancją kostną odkładaną w postaci nieregularnych zgrubień, guzków lub wałeczków. Są one oddzielone od siebie rowkami zawierającymi naczynia krwionośne, które w miarę narastania szkieletu przechodzą w kanały otwierające się porami na powierzchni. Plastyczność tego typu pokrycia sugeruje, że może ono w prosty sposób przechodzić zarówno w drobnoelementowy jak i wielkoelementowy typ pokrycia. Wielkość bezwzględna zwierząt i związana z tym grubość skóry, proporcje kości czołowych a także stopień kinetyzmu czaszkowego to czynniki mogące wpływać na charakter pokrycia osteodermalnego, które tłumaczą jego zmiany w filogenezie. Jego stabilność w obrębie rodzin związana jest głównie ze stabilnością wyżej wymienionych cech kraniologicznych. Proponowana przez niektórych badaczy homologia pomiędzy wielkoelementowym pokryciem osteodermalnym czaszki u Scincomorpha i Anguimorpha interpretowana jest tutaj jako homologia pokrycia epidermalnego, które przypuszczalnie jest wspólną cechą pochodną (shared derived, synapomorphic) wyjściową dla obu taksonów. Zarówno wielko- i jak i drobnoelementowe pokrycia osteodermalne stanowią stany pochodne poszczególnych szczepów. Wysunięto przypuszczenie, że pokrycie wielkoelementowe nie wytworzyło się u Anguimorpha przed zróżnicowaniem się głównego pnia na nadrodziny Platynota i Diploglossa. Jego pojawienie się jest przejawem paralelizmu ewolucyjnego w obu pniach Autarchoglossa.

Ustalony na podstawie zasady powszechności (out-group analysis) oraz wspólnych cech pochodnych typ wyjściowy dla Autarchoglossa powinien charakteryzować się następującymi cechami: małą wysokością i słabym nachyleniem supraoccipitale, słabym połączeniem metakinetycznym, dużą rozciągłością parasphenoidu do tyłu, brakiem processus alaris, podstawą czaszki o szeroko rozłożonych skrzydłach bocznych, obejmujących recessus vena jugularis, oraz trójkątną brzuszną powierzchnię wyrostka przypotylicznego, a także skierowaniem tylnego wyrostka prooticum do dolnego nie zaś do górnego kąta wyrostka przypotylicznego. We wszystkich szczepach jaszczurek zachodzą równolegle, choć w innym czasie, te same zmiany polegające na zwężeniu bocznych skrzydeł podstawy czaszki, rotacji przedniej powierzchni wyrostka przypotylicznego i przesunięciu prooticum ku jego górnej części. Polegają one również na skróceniu centralnej części parasphenoidu i wytworzeniu processus alaris.

Ewolucja badanego w niniejszej pracy odcinka filogenezy Autarchoglossa została przedstawiona w kategoriach stopni morfologicznych — gradów. To ujęcie zostało podyktowane stwierdzonym w wielu przypadkach powstawaniem cech na drodze ewolucji równoległej, która szczególnie dobrze tłumaczy mozaikowość budowy w pewnych rodzinach, a także brakiem rozstrzygających danych pozwalających na ścisłe odtworzenie filogenezy. Nie znaczy to jednak, by żaden spośród trzech wyróżnionych tu gradów nie mógł okazać się grupą monofiletyczną.

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CONTENTS

INTRODUCTION

The present paper is a study of Late Cretaceous Anguimorpha and their closest relatives from the territory of the Mongolian People's Republic. It is based on the material assembled by members of the Polish-Mongolian Palaeontological Expeditions to the Gobi Desert between 1963—1971.

The Upper Cretaceous Mongolian fauna containing lizards had first been found by the Central Asiatic Expeditions of the American Museum of Natural History in the locality of Bayn Dzak (referred to as Shabarakh Usu in American literature). The lizards coming from this locality (9 specimens) have been described by GILMORE (1943) along with Tertiary lizard material collected by the same expeditions from other localities of Mongolia.

The collection of the Polish-Mongolian Palaeontological Expeditions comes from the Djadokhta Formation of ?upper Santonian and/or ?lower Campanian age (locality of Bayn Dzak first explored by Americans); from the Barun Goyot Formation (localities of Khulsan and Nemegt) of ?middle Campanian stage and from the red beds of Khermeen Tsav (locality of Khermeen Tsav II), which are the biostratigraphic equivalent of the Barun Goyot Formation (see GRADZIŃSKI *et al.* 1969; GRADZIŃSKI and JERZYKIEWICZ 1972 and GRADZIŃSKI *et al.* 1977)[1]. This collection amounts to about 300 specimens of skulls, skull fragments and postcranial skeletons and is, thus, one of the largest lizard collections of Mesozoic Sauria known do date. It includes representatives of all saurian infraorders of which Scincomorpha and Anguimorpha are best represented. From this material four new genera and six new species of Scincomorpha have been described by SULIMSKI (1972, 1975, 1978). The material described in the present paper, consisting of about 20 specimens, mainly skulls, is assigned to eight genera of which seven are new. Six of them belong to the Platynota and the remaining two are primitive lizards only tentatively connected with Anguimorpha because of some anguimorphan character states they display, but are here suggested as having reached a preanguimorphan grade. Neither the present material nor GILMORE'S (1943) Late Cretaceous collection include any representatives of the Diploglossa (Anguioidea) which are so far unknown from the Late Cretaceous of Asia. A supposed anguid *Isodontosaurus gracilis* of GILMORE (1943) does not, in fact, belong to the Anguimorpha, if correctly figured by the author. On the other hand, in the Late Cretaceous sediments of North America (Wyoming, Lance Formation; Montana, Hall Creak Formation) this superfamily had diversified into different families and genera (ESTES 1964) of which *Odaxosaurus* was probably ancestral to both the Anguinae (MESZOELY 1970) and the Glyptosaurinae (MESZOELY, ESTES, HAUBOLD 1978). The Diploglossa first appeared in Asia

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[1] Recently KARCZEWSKA and ZIEMBIŃSKA-TWORZYDŁO (1983) claimed on paleobotanical evidence that the Nemegt Formation which overlies conformably the Barun Goyot Formation is not younger than the equivalent of the lower Campanian stage. Therefore, the Barun Goyot Formation (and the red beds of Khermeen Tsav) may be of ?late Santonian and the Djadochta Formation of ?early Santonian or ?late Coniacian age. These estimates should be regarded as tentative.

in the Late Eocene Shara Murun Formation (*Glyptosaurus* near *nodosus* according to GILMORE 1943), called *Helodermoides mongoliensis* SULLIVAN 1979 and referred to as *Placosaurus* by ESTES 1981) and are supposed to be allochtonous on this continent. In contrast, the Platynota are represented in both America and Asia but the data are inconclusive for the determination of the mutual relations of both faunas.

Since the present material consists mainly of skulls and skull fragments, my intention here is a phylogenetic reconstruction relying primarily on cranial characters. Variability of the latters within the infraorder Anguimorpha, their ranges and discontinuities are thus my main interests. Incomplete and poorly preserved fragments of the postcranial skeletons will be studied elsewhere along with other postcranial materials.

The present systematics of the suborder Sauria is mostly the work of CAMP (1923) (the earlier attempts are broadly discussed in the same paper) supplemented by ROMER (1956) on the basis of detailed osteological investigations of various authors covering the period from 1923 till 1956. The main subdivision of Sauria into four stems (the sections of CAMP 1923, the infraorders of ROMER 1956) is generally accepted, whereas their mutual relationships are still subject to discussion. Anguimorpha and Scincomorpha are commonly regarded as closely related groups (division Autarchoglossa of CAMP'S classification) but the union of Iguania and Gekkota within one division Ascalabota is no more valid (ESTES 1982).

The head skeleton of anguimorphan lizards has been mentioned and discussed in a number of more general lizard papers, such as COPE (1864, 1892), SIEBENROCK (1892), CAMP (1923), LAKJER (1927) as well as in more detailed papers concerning only the representatives or groups pertaining to this infraorder, such as FEJÉRVÁRY (1918, 1935), MERTENS (1942), BARROWS and SMITH (1943), TOERIEN (1950), McDOWELL and BOGERT (1954) and RIEPPEL (1981), the last two being extensive monographs on the infraorder. A knowledge of the infraorder has also been much increased by purely paleontological papers, such as GILMORE (1928, 1943), HOFFSTETTER (1943, 1964, 1967), ESTES (1964), MESZOELY (1970) and SULLIVAN (1977) discussing the status of various fossil forms.

JOLLIE (1960) summed up current knowledge of the lizard skull with a view to stressing the consistency of pattern within the group rather than divergence in the phylogeny. He indicated the limits of variation in major skull features within the range of the suborder, but was rather sceptical about the use of this variation for defining the major lacertilian categories. In fact, skull characters other than tooth development, osteodermal covering and structure of the hyoid apparatus have not usually been used for lizard taxonomy above the family level.

ROMER (1956) was the first to give an extensive synopsis of the skull characters for each infraorder of Sauria. This must be understood as only an indication of the most common skull character states, since the variability of the characters is not defined but merely its existence is suggested, it being probable that overlapping of variability ranges (mentioned by JOLLIE 1960) does occur. In fact overlapping of the variability ranges cannot be avoided in most of the characters when two closely related groups are studied, the amount of overlap increasing the more subunits are included in the analysis and the older their common ancestry becomes. The study of the peripheral subunits of the taxon, i. e. the subunits least closely related to those remaining, is of importance for making precise the true limits of variability, as well as in determining the derived features of the studied taxon shared by its subunits. That is why the two families Bainguidae nov. and Paravaranidae nov. are included in the present paper although they cannot be conclusively included in the infraorder. They tend to describe the peripheries of this taxon.

The methodology used in the present paper is derived from cladism in that (1) the character states are analyzed in terms of primitive and derived, (2) the polarity of characters is determined through the morphological criteria, (3) the hypotheses are constructed in the form of character distributions figured as cladograms, (4) the phylogenetical and taxonomical inferences are drawn from the relative recency of the common ancestry shown by a character distribution. In order to make the cladograms as informative as possible the character states are superimposed in the form of labelled nodes. Each node refers to the whole section of the cladogram superior to the bifurcation situated directly below it, unless a further change is indicated.

TERMINOLOGY AND ABBREVIATIONS

Terminology used in the present paper is mainly that of Oelrich (1956) except for the following: „mandibular fossa" of Jollie (1960) is used instead of „mandibular foramen" of Oelrich and „suborbital fenestra" and „parietal foramen" of Romer (1956) instead of „inferior orbital foramen" and „pineal foramen" of Oelrich. „Subolfactory processes" is a term used by McDowell and Bogert (1954) for the descending processes of frontals.

Terminology referring to the skull kinesis is after Frazzetta (1962), though the term „hypokinetic axis" comes from Russell (1964). New terms: „sphenoccipital torus" (p. 72) and „lateral ridge" (p. 74) are introduced to denote elements of sculpture of the brain case surface connected with muscle insertions (see fig. 22). The term „osteodermal skull covering" is used to designate all kinds of dermal skeleton deposited within the skin over the dermal skull roof and varying from a slight incrustation of bone to a thick layer of bone referred to as an armour. „Segmentation zone" is introduced to denote the lateral part of the frontal region in which the osteodermal skull covering is, as a rule, subject to multiplication. „Parasagittal zone" denotes the parasagittal part of the frontal region characterized by an intimate adhesion of the skin. Lumpy surface denotes parts of the osteodermal skull covering prominently sculptured with grooves and striations as exemplified by *Parasaniwa wyomingensis* (Estes 1964, fig. 63).

Abbreviations:

ectpt = ectopterygoid, for. = foramen, j = jugal, pmx = premaxilla, pt = pterygoid, qu = quadrate, quj = quadratojugal, v = vomer.

AMNH	The American Museum of Natural History, New York
HUB	Zoological Museum of Humboldt University, East Berlin
BMNH	British Museum (Natural History), London
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
PIN	Palaeontological Institute, USSR Academy of Sciences, Moscow
UW	Warsaw University
ZIN	Zoological Institute, USSR Academy of Sciences, Leningrad
ZPAL	Institute of Paleobiology, Polish Academy of Sciences, Warsaw

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paleontology of Sauria. Dr ESTES has kindly reviewed my manuscript. His critical comments helped me a great deal in the preparation of the final version of the manuscript. Since, however, I did not follow all his sugestions I am the only one responsible for the errors of this paper.

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SYSTEMATIC PART

Suborder **Sauria** Mc CARTNEY, 1802

PREANGUIMORPHAN GRADE

Definition. — Early autarchoglossan lizards having primitive brain case structure. Recessus vena jugularis broad and largely ventrally exposed. No alar process of prootic. Sphenoccipital contact variable. Splenial not shortened anteriorly.

Discussion. — The preanguimorphan grade is introduced to embrace the lizards which cannot be included into the Anguimorpha *sensu stricto* because of their primitive brain case structure but which still display some anguimorphan features of teeth, mandibles and maxillary segments of skulls. These genera tend to corroborate the hypothesis proposed in the present paper that (1) the development of a long, anteriorly extended alar process and the narrowing of the distal part of the paroccipital process associated with a dorsal shift of the posterior part of the prootic crest (see p. 75), alongside the development of the trapezoidal sphenoccipital suture are shared derived character states of the Platynota and the Diploglossa acquired by their common ancestor, and that (2) this ancestral stage was preceded by a more primitive stage of anguimorphan evolution, at which an adaptive radiation occurred. The intermediate tooth replacement tending to the varanid pattern would be a shared and derived feature in the resulting groups.

The systematic position of the genera here included is far from being clear. *Paravaranus* shows striking similarities to the Platynota (here interpreted as a convergence). The exclusion of this genus from the Anguimorpha *sensu stricto* is in accord with my opinion that the structure of the brain case and certain features of the mandible were attained earlier in the evolution of the *Platynota* than the form of the maxillary segment.

The determination of the systematic position of *Bainguis* is even more difficult, if based on the skull structure only. Its tooth replacement is not of varanid type (although one of its mandibles, pl. 3 : 2a, suggests this) and no one of its anguimorph features (see p.) is important enough to indicate firmly its anguimorphan relationships. It has some lacertilian features instead (p. 20). However, its primitiveness (brain case, parasphenoid, mandible) and the mosaic pattern of its structure suggest its representing a group close to the main bifurcation of the autarchoglossan stem. Its assignment may thus be only arbitrary. Therefore it is left within the preanguimorphan grade, assigned to a family of its own of the uncertain infraordinal afiliation until the investigation of its postcranial skeleton (pls. 2:2, 13:5) and new discoveries provide new data allowing a more precise assignment.

Superfamily *uncertain*

Family **Paravaranidae** nov.

Diagnosis. — Small Sauria not attaining 3 cm of skull length, with varanid tooth replacement. Teeth pleurodont without basal fluting. Retracted nares separating maxilla and anterior part of prefrontal from fused, narrow nasals. Subolfactory processes lacking. Parietal foramen situated on curvilinear frontoparietal suture, possibly variable. Postorbital joining postfrontal from lateral side, broadly entering into the orbit. Squamosal large posteriorly, broadly contacting with posterolateral part of cranial roof. No alar process of prooticum. Paroccipital process with broad, triangular ventral surface. Posterior margins of paroccipital processes forming an angle of nearly 180° with each other. Splenial almost reaching the symphysis, probably passing onto lower margin of mandible in its anterior part.

Genus assigned: *Paravaranus* gen. n.; monotypic family.

Geographical and stratigraphical range. — Khulsan, Nemegt Basin, Gobi Desert, Mongolian People's Republic. ?middle Campanian, Barun Goyot Formation.

Discussion. — The character complex of *Paravaranus* is a mixture of character states of two infraorders Anguimorpha and Scincomorpha and thus, this genus cannot be assigned to any of the known families belonging to these infraorders. Therefore, a new family Paravaranidae is created to receive this genus. Two alternative hypotheses which are discussed below (fig. 1 A and B) are, in my opinion, the best choices from various possibilities of the systematic position of the Paravaranidae. They differ from one another in basing either on a few derived character states or on a complex of plesiomorphic character states.

The possibility of the paravaranids being an offshoot of the anguimorphan stem (fig. 1 A) is first considered since the varanid tooth replacement (1′) is usually given a great taxonomic importance. A tendency to the development of this method of tooth replacement is here regarded as a shared derived character state of Anguimorpha. It is manifested by an intermediate type of tooth replacement, which is prevalent in the Diploglossa, or by a varanid type, characteristic of the Platynota (see EDMUND 1960, RIEPPEL 1978). The varanid method of tooth replacement is here considered as phylogenetically derivable from the intermediate pattern. I would hypothesize that the shift of the replacement teeth to the interdental space results from the increased spacing of teeth, advantageous to the predatory adaptation. A tendency to posterior extension of the external nares (9″) which was a basis for the development of the overall varanid appearance of the skull in the Paravaranidae ties in well with the above data to suggest the legitimacy of the first hypothesis. Although the remaining complex of characters of the Paravaranidae seems to be inconsistent with their assignment to Anguimorpha, as understood now, some of these character states can best be regarded as plesiomorphic and thus, do not exclude their representing a primitive group of this infraorder. These are as follows: large anterior extension of the splenial (2); lack of the alar process of the prootic bone and a broad, triangular, ventrally exposed distal extremity of the paroccipital process (3); lack of subolfactory processes, a curvilinear frontoparietal suture and a parietal foramen situated on this suture (5); the postorbital contacting the postfrontal from lateral and entering the orbit (6).

The acceptance of the first hypothesis would call for the indication of the exact position of the Paravaranidae within the anguimorphan stem. Some of the plesiomorphic character states of the Paravaranidae (2, 3, 5) are alternative with corresponding shared derived character states of the Diploglossa and the Platynota, and thus, may indicate that the common ancestry of the Paravaranidae with either of these superfamilies was more remote than the common ancestor of the Diploglossa and the Platynota. Illustrating this hypothesis a cladogram A (fig. 1) gives all data available on the character distribution within the evolutionary lines concerned. The earliest divergence includes the appearance of a small, primitive, predaceous autarchoglossan having a varanid tooth replacement. The structure of the sphenoccipital suture and shape of squamosal is probably primitive but unknown to me. Deriving from such an ancestor the paravaranids were subject to a varanid type of specialization. This may only be called convergence because the ancestor may not be shown to be predisposed to such a specialization in any way. Diverging from the Paravaranidae an ancestral form of the anguimorphan subfamilies proper developed some new derived character states of the brain case (3′, 4″, 5′) of the splenial (2′) as well as of the squamosal (10′).

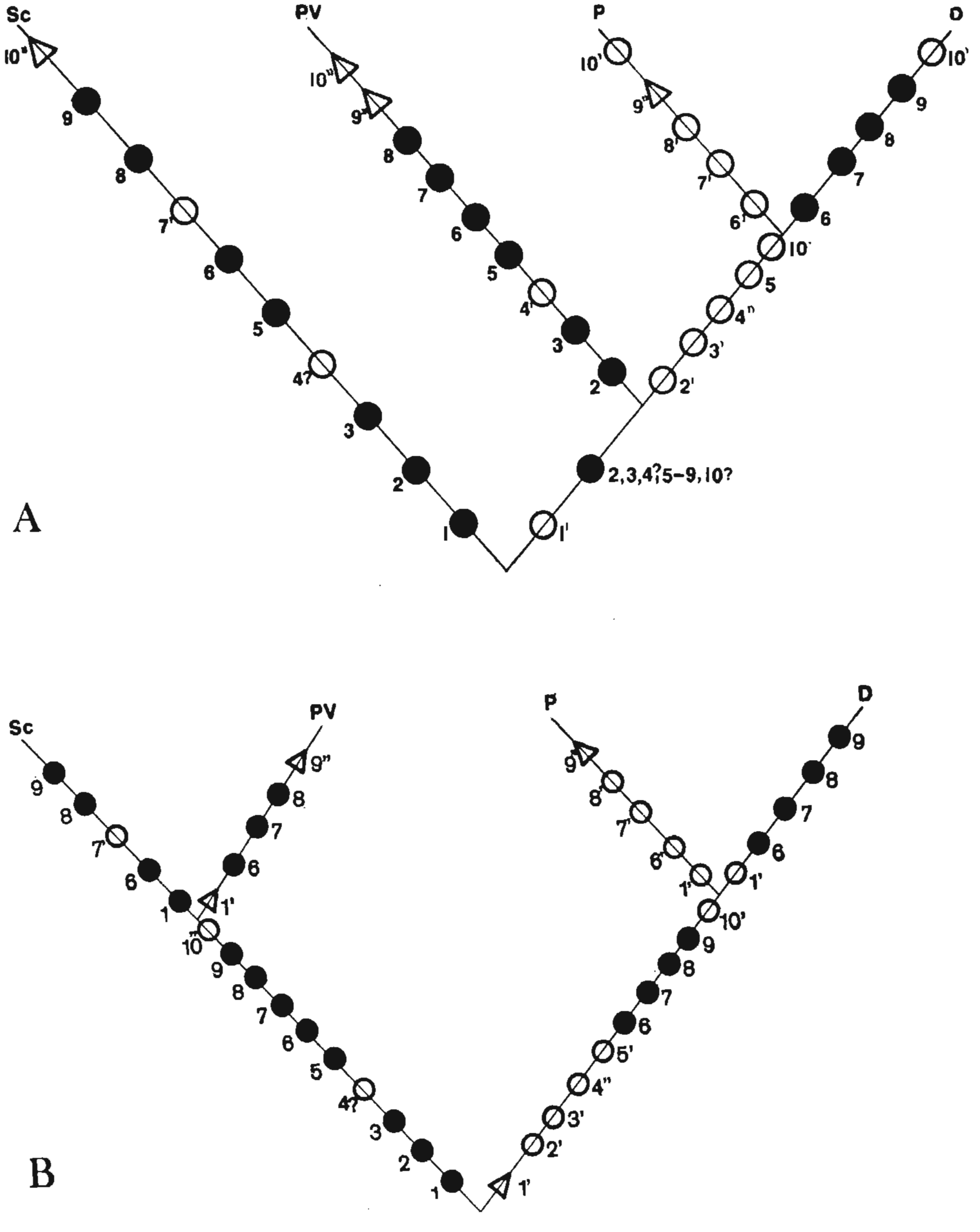


Fig. 1

Cladograms illustrating possible relationships between the Paravaranidae (PV), the Platynota (P), the Diploglossa (D) and primitive Scincomorpha (Sc). A, B-alternative hypotheses differing in method of affiliation of the Paravaranidae. Solid black circles are primitive character states; open circles are derived character states, triangles denote the states resulting from convergence. *1* Iguanid type of tooth replacement; *1'* Tendency to development of varanid type of tooth replacement; *2* Large anterior extension of splenial; *2'* Anteriorly shortened splenial; *3* Primitive brain case structure — lack of alar process of prootic; broad triangular, ventrally exposed distal extremity of paroccipital process; *3'* Derived brain case structure — tendency to development of alar process of prootic; tendency to narrowing of distal extremity of paroccipital process; *4* Primitive state of sphenoccipital suture; long parasphenoid; *4'* Angular shape of sphenoccipital suture; *4''* Trapezoidal shape of sphenoccipital suture; *5* Slight if any mesokinetic mobility — lack of subolfactory processes of frontals; variable frontoparietal suture; *5'*, *5''* Two derived states of development of mesokinetic mobility and of subolfactory processes; straight frontoparietal suture; *6* Postorbital contacting postfrontal from lateral; *6'* Contact between postorbital and postfrontal tending to specialization; *7* Small dimensions; *7'*, *7''* States of size increase; *8* Lack of basal fluting; *8'*, *8''* States of dentine folding; *9* Unretracted nares; *9'*, *9''* States of nares retraction; *10*, Posteriorly narrow squamosal; *10''* Posteriorly enlarged squamosal (probably secondary).

Worth mentioning are some similarities between the Paravaranidae and the Mosasauridae, such as a state of the frontoparietal suture and slight if any development of the subolfactory processes of the frontals (5) as well as a posteriorly broadened squamosal (10′′) recalling a secondary state of the Xenosauridae. However, with their intramandibular joint, the strong dentine folding and the modern brain case, the mosasaurs are strongly specialized but still typical platynotans, the similarities to the Paravaranidae being most probably a casual coincidence.

Interestingly enough, the whole set of character states of *Paravaranus*, recalls the Teiidae and particularly so their Late Cretaceous relatives, the Macrocephalosauridae and the Polyglyphanodontidae. The Late Cretaceous groups share following character states with the Paravaranidae: a large anterior extension of the splenial (2); a primitive state of the paroccipital process and an alar process probably variable, rudimentary, directed upwards or wanting (3); exactly the same pattern of the postorbital and squamosal regions (6 and 10′′); variable, sinuous or curved frontoparietal suture (5) with a parietal foramen situated on it (*Macrocephalosaurus*, *Polyglyphanodon*) or very close to it (*Darchansaurus*).

The above similarities point to a second hypothesis, the one affiliating the Paravaranidae upon the teiid stem (fig. 1 B). This hypothesis is mainly based on the plesiomorphic character states. However, a complex of such character states, if sufficiently numerous and not associated with each other could, according to HECHT (1976), be suggestive of a kinship. The Paravaranidae would have evolved as one of the branches resulting from an early teiid radiation. Their varanid-like appearance (9′′) and their interdental tooth replacement (1′) would, both, be regarded as convergent character states this time.

The above hypotheses (fig. 1 A and B) have one important point in common. Both assume a derivation of the Paravaranidae from a very early part of the phylogenetic tree of Sauria, directly subsequent to a bifurcation of the autarchoglossan stem, the differences between the systematics implied by them being thus reduced to a small shift. Cladogram B (fig. 1), which seems to be a more parsimonious hypothesis, implies the association of the Paravaranidae with the primitive Scincomorpha. However, this is much more risky a move, and it demands thorough studies of this group of lizards, which is out of the scope of the present paper. Besides, a very impressive platynotan adaptation of *Paravaranus* leaves room for some doubts whether the complex of character states considered is reliable for excluding the platynotan relationships of the family. In particular the state of the frontoparietal suture may be an artefact of preservation and that of the sphenoccipital suture may be a juvenile feature to be changed in adults. But other character states are not likely to be changed with age. Therefore I leave the family Paravarnidae without any infraordinal assignment, an informal unit „preanguimorphan grade" being created to designate its morphological state (see p. 11).

Genus *Paravaranus* nov.

Type species: *Paravaranus angustifrons* sp. n.

Derivation of the name: The particle (Lat.) *para* = besides is to imply that the animal is similar but not directly related to *Varanus*.

Diagnosis. — As for the family. The variability below the family level being unknown, the generic characters cannot be separated from those of the family.

Stratigraphical and geographical range. — Known only from the type horizon and type locality.

Paravaranus angustifrons[*] sp. n.

(pl. 1 : 1, 2; pl. 4 : 1, figs. 2, 3, 4a)

Holotype: Skull ZPAL MgR-I/67.
Type horizon: Upper Cretaceous, ?middle Campanian, Barun Goyot Formation.
Type locality: Khulsan, Nemegt Basin, Mongolian People's Republic.
Derivation of the name: Lat. *angustus* — narrow, *frons* — front; a lizard with a narrow front.

Diagnosis. — Characterized by overall varanid appearance of skull. Frontal fused, very narrow. Orbits very large in horizontal plane due to lateral expansion of jugal arches. Skull roof sculptured by concavities limited by ridges. Adductor musculature originating dorsolaterally on parietals. Pterygoids, bearing numerous minute teeth, wedge in between palatines reaching alomst to the vomers. Vomers Y-shaped, fused in front diverging backwards. Maxillary teeth pointed, *Anguis*-like; their bases broadened transversally, somewhat oblique to the jaw axis. Mandible low and slender.

Material. — The only specimen ZPAL MgR-I/67, the holotype, is a damaged skull lacking the anterior part of the snout. A right jugal, left paroccipital process, distal parts of the posterolateral processes of the parietal and both upper temporal arches are missing except the anterior and posterior ends of the right temporal arch which are preserved. Also preserved are: a small fragment of the premaxilla belonging to the same individual but not connected with the rest of skull, a strongly damaged right mandible without a retroarticular process, two upper and three lower teeth.

Measurements. — See Table 1.

Description. — **Skull as a whole.** The skull is roughly pentagonal in outline, its maximum width being about the middle of the orbits. The orbits are very large in contrast to a strong constriction of the frontals. External nares separate not only the maxilla from the nasals but they wedge in a small distance between the nasals and the prefrontals. The parietals are much shortened and have the origins of the mandibular adductors situated laterally on them. Supratemporal fossae are large. No osteodermal skull covering.

Skull roof. The unpaired premaxilla has a horseshoe-shaped body broader than long. Practically nothing is known about its processes. Septomaxilla is absent from the specimen. Nasals retain the traces of being paired in their posterior part which is subdivided by a sagittal ridge, but are completely fused in their anterior, abruptly narrowing part. They are all dorsoventrally flattened instead of being vertical in their distal part as they are in *Varanus*. The frontal are very slender, completely fused bones. Their minimum width about the middle of their length is 2/5 of their anterior width and 1/5 of their posterior broadening. The supraorbital ridges are thickened and dorsally projecting, the dorsal surface of the bone being concave between them. The subolfactory processes are absent except at the suture with the prefrontal; they slightly project below and behind the supraorbital processes of these bones. The frontoparietal suture is sinuous and thus forms no hinge joint. It passes through the parietal foramen, than runs forwards and laterally in two posteriorly concave semicircles.

The entire length of the parietal, with its posterolateral processes included, is about the same as the length of the frontal, but the main body of the parietal is about half its length. The surface of the parietal is subdivided into several concave parts by distinct ridges. Limiting the lateral surface for the adductor muscles a sharp crest extends over the parietal from its anterolateral corner, posteromedially to the base of the posterolateral process, than posterolaterally along this process. These crests being paired, analogous to the external parietal crests of mammals, delimit the dorsal surface of the parietal along with a transverse ridge directly comparable to the nuchal crest. This surface is subdivided into three parts by a ridge running sagittally from behind forwards, nearly to the parietal foramen then dividing into two rami and diverging towards the frontoparietal suture. Behind the posterior boundary of the dorsal surface there is a well developed muscular surface, facing backwards and upwards, which is continuous with equally well developed medial surfaces of the posterolateral processes of the parietal. The paired spinalis capitis inserted on the parasagittal and upper parts of this surface. Directly beneath its traces, separated by a rounded incision of the parietal margin, are two rounded concavities and lateral to them two other concavities extending onto the medial surface of the posterolateral processes. Since, apart from the spinalis capitis, only two pairs of muscles attach to the posterior part of the partietal in lizards (OELRICH 1956), the concavities can be interpreted as the scars of origin of the depressor mandibulae and those of insertions of the episterno-cleidomastoideus.

The lateral surface of the maxilla is flat and triangular. Its anterodorsal margin is straight, sharp and projecting dorsally over the level of the nasals to produce a concave dorsal surface of the snout. Its anteroventral part is unknown. The posteroventral angle of the maxilla is situated about at the level of the anterior wall of the orbit. The posterior limit of the maxilla and its sutures with neighbouring bones cannot be established with any certainty because of its state of preservation. The palatal shelf is narrow, tapering posteriorly without any broadening at the contact with the palatine. Its external border projects well below the parapet of the jaw.

The dorsal surface of the prefrontal is rhomboid in shape owing to the reduction of its anteromedial part caused by the extreme elongation of the external nares. This, along with the huge orbits and the large supratemporal fossae gives the skull its varanid appearance. The shorter

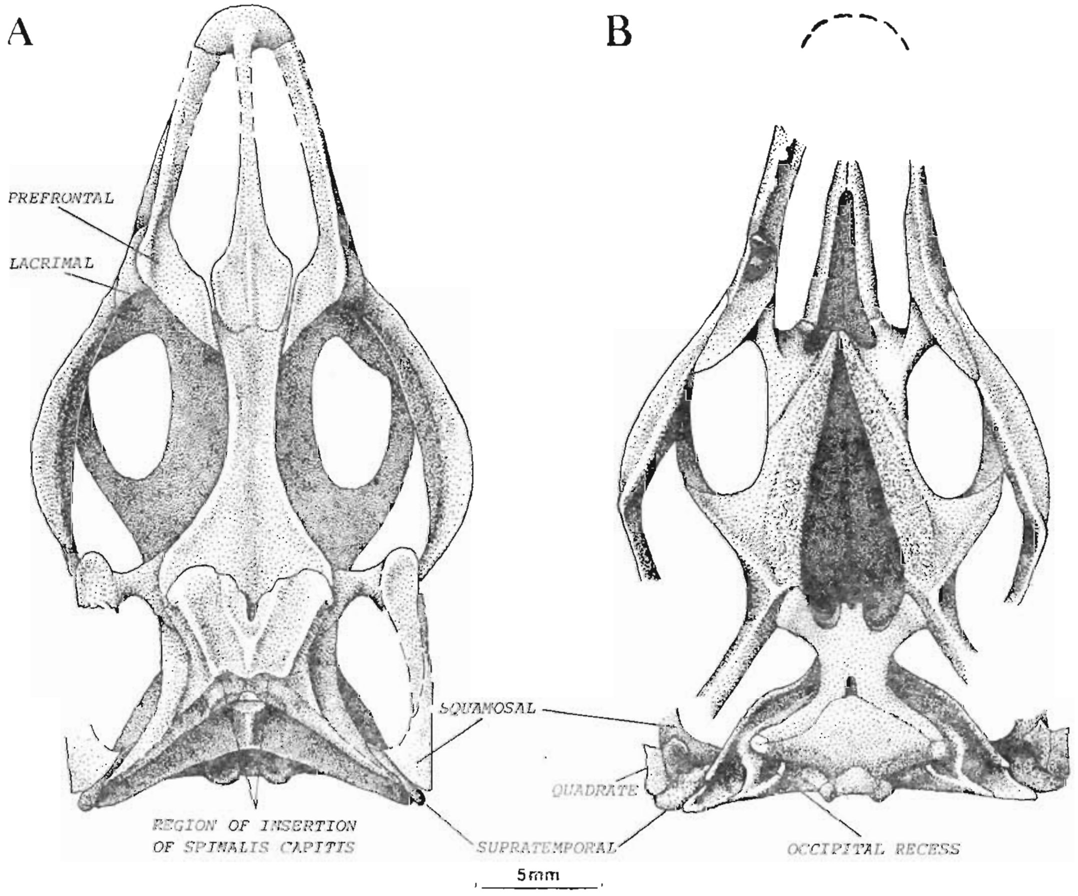


Fig. 2
Paravaranus angustifrons gen. n., sp. n. Skull. A-Dorsal view; B-Ventral view.

margins of the prefrontal extend parasagittally, the longer ones obliquely in the anterolateral direction. The lateral margin of the prefrontal strongly projects dorsally thus contributing to the formation of the prominent ridge delimiting the dorsal surface of the skull roof, which is produced mainly by the maxilla in this region. The posterior half of the dorsal lamina of the prefrontal together with the dorsal triangular part of its oribital lamina make up a supraorbital process of this bone. The latter extends back along a quarter the length of the frontal only and is widely separated from the postfrontal. The remaining subquandrangular part of the orbital lamina of the prefrontal forms a subhorizontal suture with the palatine. It has probably no contact with the lacrimal, being separated from it by a large, single, fissure-like lacrimal foramen. The lacrimal is a smal plate-like bone bearing no foramina. It contributes to the formation of the orbital rim and has two surfaces, the lateral one and the lacrimal one facing to the lacrimal canal. The jugal is a rather deep, semilunar bone tapering at both ends. Its ventral border extends horizontally, turning abruptly upwards only about posterior 1/3 of its length. The dorsal concave border has a laterally projecting rim which makes the lateral surface of the jugal concave and the medial one convex in transverse section. The anterior end of the jugal is sutured to the maxilla ventrally, to the lacrimal dorsally, to the palatine and prefrontal ventromedially. Its posterior end is broken off but it probably made a sliding joint with the postorbital (see below). The jugal arches are strongly expanded laterally and thus the jugal as a whole is laterally convex.

Medially the horizontal part of the jugal is sutured to the ectopterygoid. The jugal probably did not enter the suborbital fenestra being separated from it by the maxilla and the ectopterygoid.

The postfrontal has a short quadrangular body with four projecting corners. It is somewhat x-shaped in appearance. The length of its slender frontal process is only about 1/6 of the length of the frontal margin; the parietal process does not reach half way back on the parietal main body. The lateral margin of the postfrontal is connected (may be fused) with the postorbital along a parasagittal suture. The postorbital extends more anterior than the body of the postfrontal and contributes to the formation of the orbit. It presents two concave surfaces; one of them facing upwards and laterally is medially fused to the postfrontal. The second one facing downwards and laterally probably made a sliding joint with the jugal. The posterior part of the postorbital is not preserved.

The only preserved part of the squamosal, its posterior triangular part, broadly contacts the cranial roof by means of a sort of a dorsal process which is probably not homologous to the dorsal process of Iguania, Eolacertilia (ROBINSON 1967) and Paliguanidae (CARROLL 1975) but is a secondary, medial broadening instead.

Palatal complex. Vomers are rod-like bones fused in front diverging backwards. The most anterior, fused part of the bone is broken off and thus its relations to the surrounding bones cannot be established.

The palatine consists of a subquandrangular body and three processes. Vomerine and maxillary processes project from two lateral angles of the quandrangle and the third, or pterygoid process, projects from the medial side of this quandrangle. The vomerine process, well separated from the remaining bone, rounded in transverse section, is more dorsal and reaches slightly more anterior than the maxillary process. The pterygopalatine suture is a straight line extending obliquely anteromedially. The pterygoid process is overlapped by the pterygoid, which could probably slide over it (see pl. 1 : 1c). The vomeropalatine and a maxillopalatine sutures probably also permitted a certain amount of movements. The dorsal surface of the palatine does not ascend to any important degree to meet the prefrontal but is almost flat instead.

The palatine process of the pterygoid is a flat, elongated bone blade tapering in front. It is covered by numerous small teeth all over its length, only a narrow lateral zone being deprived of them. The transverse process is a triangular plate ventrally concave. Projecting ventrally from its posterolateral margin is a distinct crest, probably for origin of the pterygomandibularis. No projecting process for this muscle is formed in this region. The pterygoectopterygoid suture has a transverse course and the ectopterygoid is situated completely in front of the ectopterygoid process of the pterygoid. The quadrate processes are not preserved except for the anterior part of the left one. Extending from in front of the basipterygoid articulation, posterolaterally along the quadrate process, is a distinct crest bordering the basipterygoid articulation from its ventral side and separating the medial surface of the quadrate process from the lateral one.

The ectopterygoid is a small semilunar bone making up the posterolateral limit of the suborbital fenestra. It probably reached the posteroventral angle of the maxilla at about half the length of this foramen but its exact extension cannot be established due to the damage.

The epipterygoid is missing from the specimen. The columellar fossa of the pterygoid destined for the base of the epipterygoid is an elongated furrow rather than a circular fossette. The preserved dorsal extremity of the right quadrate indicates the oblique position of this bone in the resting phase of the jaw apparatus.

Occipital segment. Extending from a posterodistal corner of the basipterygoid processes almost to the top of the sphenoccipital tubercles, sharp ventrolateral crest projects laterally to separate a flat ventral surface of the basisphenoid + parasphenoid from its lateral parts. The posterolateral extensions of the parasphenoid reach much further posteriorly than the body to contribute to the spenoccipital tubercles. The sphenoccipital suture has a shape of a broadly opened V posteriorly concave. It cuts the sphenoccipital tubercle almost to the cap formed by the epiphysis (fig. 2, pl. 1 : 1e). At the top of this angular suture there is an oval fontanelle, its longer axis, about half the length of the sphenoid part of the brain case, directed sagitally. This character state suggests a young age of the specimen but in view of the advanced state of ossification of the skull as a whole it rather points to the retardation of the ossification of the basisphenoid in ontogenesis or to its shortness, which seems to be a primitive condition (see p. 72). The fontanelle is laterally bordered by lateral parts of the parasphenoid failing to fuse with each other. It recalls a young individual of *Calotes jubatus* (LAKJER 1927, fig. 8a) very much.

The basipterygoid processes have long and slim peduncle projecting laterally and, to a high degree, anteriorly but almost not at all ventrally. The dorsolateral margins of a broad base of the anterior parasphenoid process are connected to the anterodorsal parts of the basipterygoid processes by bone blades situated deep to the ventral surface of the basisphenoid and ventrally concave. The presence of the Vidian canal aperture within these concavities cannot be ascertained.

The ventral surface of the basioccipital is flat. It abruptly bends in its posterolateral parts to pass into the posterior walls of the sphenoccipital tubercles. The lines of bending converge from the tops of the sphenoccipital tubercles towards the middle of the posterior margin of the occipital condyle and they correspond to the sphenoccipital torus (see p. 72). Parallel to this line the suture between the basioccipital and the exoccipital cuts transversally the region destined for the rectus capitis anterior. This flat region faces posteroventrally and is not separated from the superior part of the exoccipital by any crest corresponding to the lateral ridge. Running ventrolaterally, a short distance from the upper margin of the foramen magnum is a sharp crest separating the posterior surface of the exoccipital (probably a region of insertion of the rectus capitis posterior) from the posterior surface of the paroccipital process facing posterodorsally and probably receiving the obliquus capitis.

The occipital condyle is clearly tripartite. Its basioccipital part is subtriangular in ventral aspect. Lateral of the large rounded occipital foramen at the level of the lateral part of the occipital condyle is a hypoglossal foramen and just superior to it a vagus foramen, both lying in a semilunar furrow laterally concave.

The prootic crest extends from beneath the inferior process upwards and backwards. Behind the anterior semicircular canal its course is almost horizontal and the same level as the lower margin of the paroccipital process. It follows the course of the horizontal semicircular canal. The recessus vena jugularis is very broad and shallow and faces ventrolaterally. Posteriorly it passes into a horizontal, triangular ventral surface of the paroccipital process. About half the length of the recessus vena jugularis, just anterior to the foramen ovale, there is a swelling of the brain case wall containing the internal ear cavity. The alar process is not developed. The region of the prooticosupraoccipital suture is badly damaged. The contact between the brain case and the parietal seems to be rather loose.

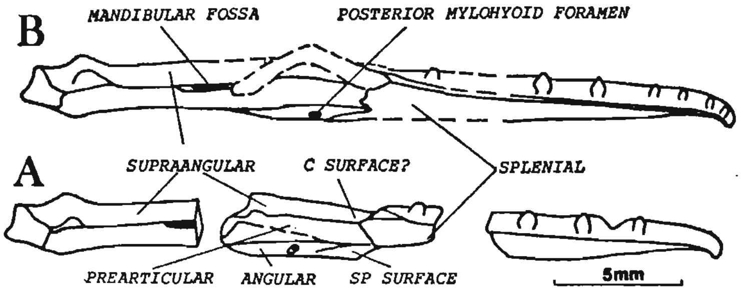


Fig. 3

Paravaranus angustifrons gen. n., sp. n. Mandible. A-Preserved parts; B-Reconstructed, medial view.

Mandible. The mandible is long and slender with a probably straight ventral border. The tooth bearing border has no subdental ridge. The splenial reaches far anterior. Its lower border makes up the lower border of the mandible, the dentary not projecting below it. The posterior extension of the spenial is reconstructed from the outline of the sp surface (figs. 3, 29). There is probably a certain coronoid overlap on the dentary but this is far from being clear. The reconstruction of the coronoid (fig. 3) is hypothetical, its extension from the mandibular fossa to the dentary being the only evidence. Curiously enough, the upper wall of the supraangular is worked into a concavity facing dorsolaterally instead of simply sloping dorsomedially as this wall usually does. It is situated at about the level of the anterior limit of the mandibular fossa. This surface suggests a presence of some overlapping bone, the only possibility, but rather doubtful, being the coronoid.

Dentition. — Neither in the maxilla nor in the dentary can the number of teeth be established. The teeth are pleurodont and conical in shape. The lower teeth are narrowed at the bases, whereas the upper ones have their bases broadened somewhat obliquely to the jaw axis. The lower teeth are very widely spaced which suggests the interdental tooth replacement. This cannot be positively stated in the upper tooth row.

Superfamily *uncertain*
Family **Bainguidae** nov.

Diagnosis. — Small Sauria about 3 cm of skull length. Tooth replacement intermediate between varanid and iguanid type. Teeth pleurodont without basal fluting. Frontals paired with developed subolfactory processes. Parietal not extended posteriad to underlay anterior body osteoscutes. Osteodermal skull armour of shield type. Body osteoscutes overlapping anteroposteriorly and sutured laterally. Parietals broad but adductor musculature originating lateral and not ventral on them. Squamosal rod-like parallelling the posterolateral extension of parietal. Prootic lacking alar process. Paroccipital process with broad triangular ventral surface. Posterior margins of paroccipital processes forming an angle of nearly 180° with each other. Parasphenoid reaching very far posterior under basioccipital. Splenial reaching far anteriad probably shifted to the lower margin of mandible in its anterior part. Limbs not reduced.

Genus assigned: *Bainguis* gen. n.; monotypic family.

Geographical and stratigraphical range. — Bayn Dzak, Gobi Desert, Mongolian People's Republic. ?upper Santonian and/or ?lower Campanian, Djadochta Formation.

Discussion. — Two possibilities can be considered as regards the affiliation of *Bainguis* since its shield-like skull armour fits both Scincomorpha and Anguimorpha, the scale pattern being rather lacertid in type. Only one character state of this armour directly points to the anguimorphan relationship of the genus. This is a lack of a posterior extension of the parietals in their parasagittal, posterior portion, which can, however, be primitive for both the infraorders.

The association of *Bainguis* with Anguimorpha is endorsed by following character states of its mandible and teeth which are supposed to be shared derived for this infraorder but probably may also occur outside it. There is no dental gutter, the tooth bases being largely exposed lingually; The Meckelian groove turns ventrally in its anterior part; the splenial is presumed to be much shortened posteriorly and not to reach behind the anterior ramus of the coronoid. The teeth are rather dense in the jaw. The presence and a rather advanced state of the subolfactory processes of the frontals which constitute another point of similarity with Anguimorpha will be discussed below. By its size and overall skull adaptation *Bainguis* recalls the representatives of the Anguidae but differs from them by scale pattern. The exact position relative to the infraorder Anguimorpha is designated by a complex of three character states. These are as follows: the extremely long anterior extension of the splenial (pl. 3 : 2a, fig. 6), the lack of the alar process of the prootic (fig. 4C) and an extremely primitive state of the parasphenoid (fig. 20J). Of these character states the first and the second one are accepted by a cladogram A (fig. 1) for the early Anguimorpha, but the state of the parasphenoid is rather eosuchian level not known in any other Sauria. It tends to shift the Bainguidae outside the Anguimorpha. They would represent a side branch separated from the autarchoglassan stem prior to stabilization of the brain case type. The development of the subolfactory processes of the frontals which is completely out of place at this early stage of evolution should be recognized as an independent acquisition of the Bainguidae (autapomorphy) and should not be used as the case for the anguimorphan nature of the family. The establishment of the systematic position of the Bainguidae has some bearing on the decision concerning the status of *Paravaranus* (see. p. 14). The assignment of the Bainguidae to Anguimorpha tend to confirm the existence of a stage of primitive skull and mandible characters in the phylogeny of this infraorder (fig. 1A, section xx), this stage being represented by two branches of radically different adaptations. A position outside the anguimorphan stem would make the second possibility (fig. 1B) more probable. These two families having been removed from Anguimorpha, this infraorder becomes much more consistent. I would accept this formal solution by creating the preanguimorphan grade (see p. 11) outside the infraorder Anguimorpha to be revised with new material coming.

Bainguis gen. n.

Type species: *Bainguis parvus* sp. n.

Derivation of the name: *Bainguis* is a superficially anguid-like lizard from Bain Dzak. The particle An is replaced by Bain.

Diagnosis. — Genus monotypic. See diagnosis for the type species.

Stratigraphical and geographical range. — Known only from the type horizon and type locality.

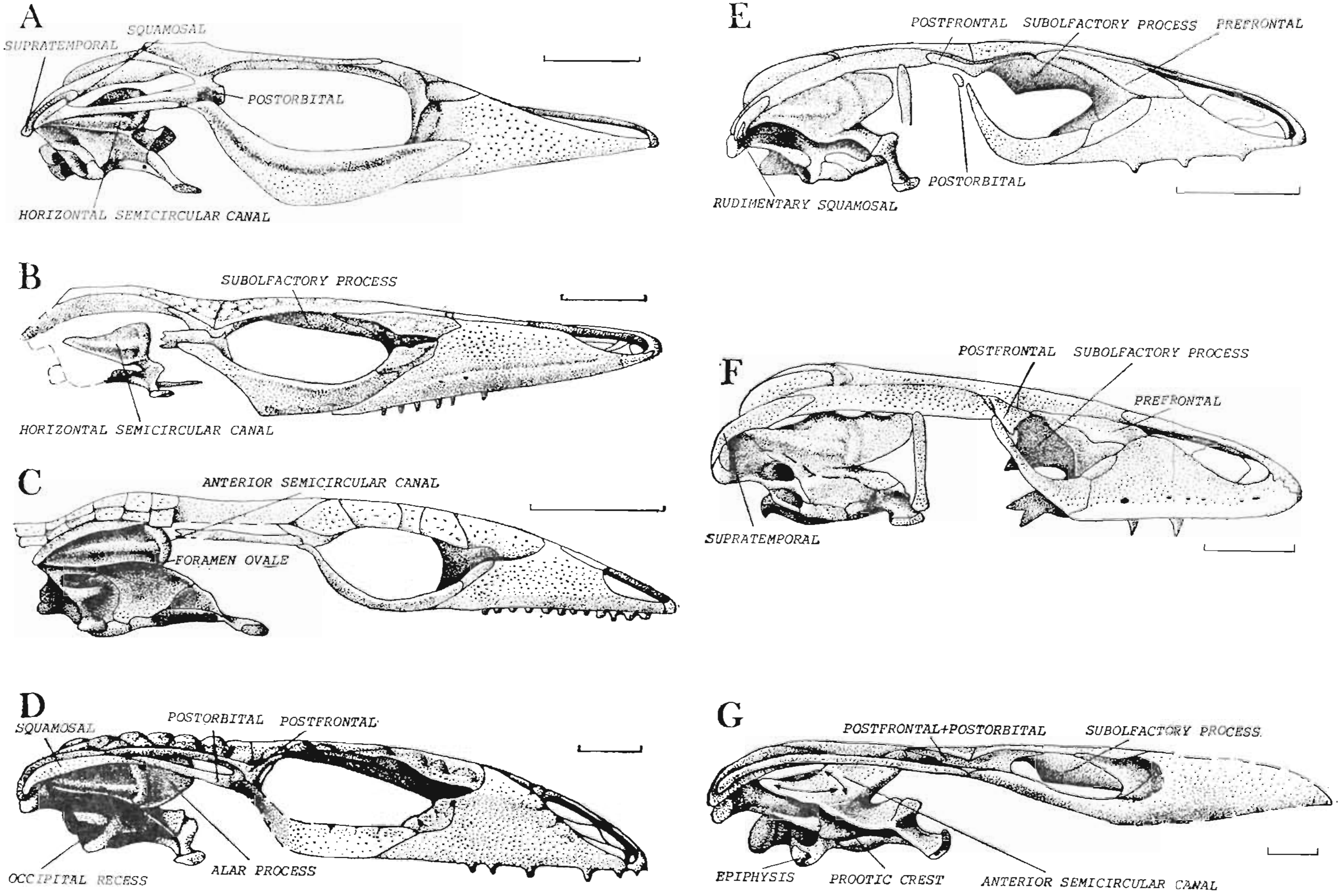


Fig. 4

Skulls in lateral view. A-*Paravaranus angustifrons* ZPAL MgR-I/67; B-*Proplatynotia longirostrata* ZPAL MgR-I/67; C-*Bainguis parvus* ZPAL MgR-II/46; D-*Gobiderma pulchra* ZPAL MgR-III/64; E-*Cherminotus longifrons* ZPAL MgR-III/59; F-*Lanthanotus borneensis* MCZ 8305; G-*Telmasaurus grangeri* ZPAL MgR-I/65. Scale 10 mm.

Table 1

Dimensions of skulls of *Paravaranus angustifrons* and *Bainguis parvus* in mm

Species and ZPAL cat. nos.	*Paravaranus angustifrons* MgR-I/67	*Bainguis parvus* MgR-II/46	*Bainguis parvus* MgR-II/90
Skull as a whole			
Condylo-basal length	e. 27	ca. 22	—
Total length	—	ca. 22	14
Length of posterior skull unit (or maximum parietal length)	e. 9	ca. 7	5.5
Length of snout unit	e. 18	ca. 15	e. 8
Length of external nares	e. 7	—	—
Maximum width over the premaxillary	—	e. 2	—
Maximum width over jugal arches	16	—	5
Width of postorbital region	11	e. 9	5
Maximum overall width	16	e. 10	5
Posterior depth	6	5.5	2
Depth anterior of orbits	3	ca. 3	1
Frontals			
Sagittal length	10	e. 7.5	4.5
Anterior width	2.2	e. 3.5	2
Posterior width	6	—	3.3
Minimum width (about the middle)	1.1	2.2	1.6
Parietals			
Sagittal length	3.5	e. 5	—
Maximum length	9	e. 8.3	—
Minimum width	5.5	ca. 5	—
Minimum distance between external parietal crests	3.1	ca. 4.5	—
Maximum posterior width	7	—	—
Brain case			
Posterior depth (metakinetic joint — ventral surface of the occipital condyle)	5	—	2
Distance between paroccipital processes	15	9.1	5
Length in ventral aspect (occipital condyle to the basis of anterior parasphenoid process)	6.5	ca. 7.5	—
Vomer			
Maximum length	>5	—	—
Maximum width	0.5	—	—
Quadrate			
Length of shaft	—	5	2.5
Width of distal condyle	—	2	1

Bainguis parvus sp. n.

(pls. 2 : 1, 3, figs. 4c, 5, 6)

Holotype: A skull ZPAL MgR-II/46.
Type horizon: Upper Cretaceous (?upper Santonian and/or ?lower Campanian), Djadokhta Formation.
Type locality: Bayn Dzak, Gobi Desert, Mongolian People's Republic.
Derivation of the name: Lat. *parvus* — small.

Diagnosis. — Skull length not attaining 3 cm. Frontoparietal scales broadly contacting medially and invading the frontoparietal suture. Skull osteoscutes thin and smooth with scarcely perforated surface. Body osteoscutes rectangular, longer than thin.

Material. — The holotype is a strongly damaged skull lacking the premaxillary, the nasals (apart from the lateral border of the right one), the supraorbital of the left side, both jugal arches, supratemporal arches and the pterygoids. Left border of the left frontal and most of the anterior part of the parietals are strongly damaged. The sphenoid part of the brain case is badly crushed and flattened. The teeth are difficult to be prepared and studied.

A juvenile skull ZPAL MgR-II/90 is assigned to the species on the basis of proportions and disposition of the quadrate identical with the type specimen, the same overall proportion of the skull and mandibles.

ZPAL MgR-II/9, 10 and 11 are fragments of a postcranial skeleton and body osteoscutes, assigned to the species on the basis of the identity of the body osteoscutes with those of the type specimen.

Measurements. — See Table 1.

Description. — **Skull as a whole.** The skull is rather long and slender with a frontal region broadened by a paired set of four simple supraorbitals, the frontals not being very broad themselves. Relative to their moderate breadth the frontals are very long connected with the elongation of the orbital part of the skull. The rostral part of the skull along with the external nares are presumed to be elongated as well. As reconstructed from the preserved posterior part of the squamosal and from the almost straight outline of the lateral border of the parietal, the supratemporal fossa was very narrow and the supratemporal arch very fine. The osteodermal skull covering is very thin. It is missing from most of the parietals. The imprints of the frontoparietal scales are hardly recognizable on the frontal surface. They are presumed to cover the posterior part of the frontals and to invade the frontoparietal suture as they do in the lacertids and gerrhosaurids, whereas the interparietal scale extends behind this suture. The anterior limit of the frontoparietal scales is reconstructed (fig. 5) on the basis of a slight furrow running over the bone surface posteromedially from about the suture between the second and the third supraorbitals. A small osteoderm situated directly lateral to the frontoparietal scute is presumed to represent the lateral part of the frontoparietal scales in other lizards. Posterior to it is a parietal scute and three small scutes of the same type as the body osteoscutes, all covering the lateral border of the parietal.

Skull roof. The nasals are reconstructed from their preserved part as long quadrangular bones suturing with the prefrontals and the maxillae. The frontals are paired. The width of the right frontal about the midlength to its length is 1 : 9 (about 1.5 : 9 in the juvenile specimen). It broadens just anterior to the frontoparietal suture. This broadening cannot be exactly determined due to the osteodermal covering; in the juvenile specimen it is about twice the minimum width. The subolfactory processes are developed as fairly deep and long plates on both specimens. They do not fuse beneath the olfactory tracts. The length proportion of the frontals, the main body of the parietal and its posterolateral extension is 9 : 5 : 3. The posterolateral extensions of the parietals are very slender and the posterior parietal border is large and straight between them. The nature of the supraoccipitoparietal joint cannot be determined because of the body osteoscute entering the posterior notch. Nor can the presence or abscence of the parietal foramen be stated owing to the damage. The parietals are large and flat. Most of their dorsal surface is horizontal, while sloping ventrolaterally just at their lateral margins. This region, which is not dorsally delimited by any distinct crest (external parietal crest), passes posteriorly into the lateral surface of the posterolateral extension of the parietal and produces a surface for the mandibular adductors.

The maxilla has a distinct nasal process extending over the dorsal surface of the snout. Anteriorly it turns ventromedially to enter the fenestra exonarina. Its posterior extent is unknown. The tooth row probably extended a little bit under the orbit. The palatal shelf, about the width of the tooth row, extends horizontally superior to the tooth bases. On the lateral surface of the maxilla, superior to the tooth bases, is a series of rounded superior labial foramina. The prefrontal makes up an important part of the dorsal skull roof lateral to the nasals and frontals. Lateral side of its long and fine orbital process is covered by the anterior supraorbital scute. Just anterior to it the surface of the prefrontal has a rounded osteodermal incrustation overhanging its orbital surface which is, in turn, produced into a furrow. From the lateral side, this furrow is delimited by a small elongated lacrimal overlapping the maxilla. The lacrimal has a concave lateral surface. The number of lacrimal foramina cannot be determined. As shown by the specimen ZPAL MgR-II/90, not covered by osteoscutes, the postfrontal is probably a narrow bone bar closely adjoining the frontal and the parietal and deprived of the jugal process. A long and very fine jugal preserved at this specimen probably loosely touched the postfrontal instead of firmy joining it. A very narrow supratemporal arch is reconstructed from remnants of the squamosal and postorbital.

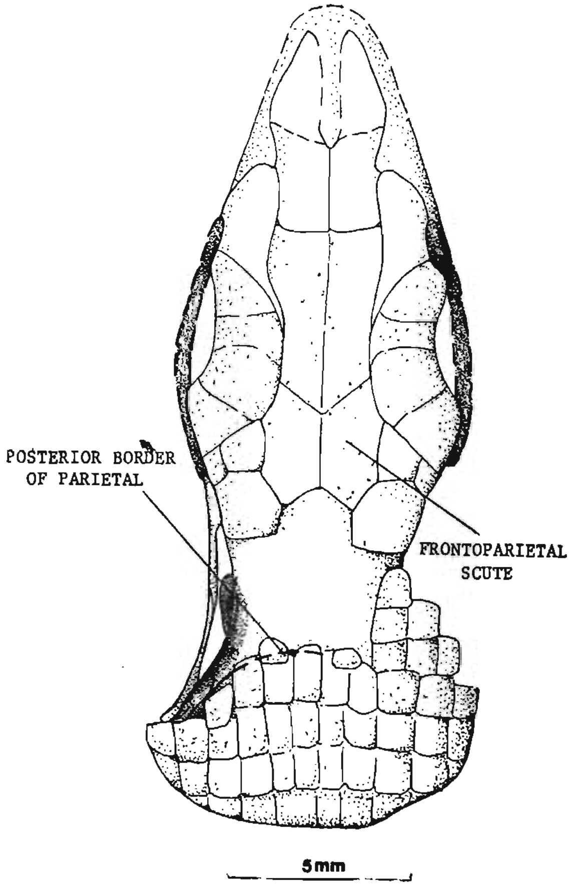


Fig. 5
Bainguis parvus gen. n., sp. n. Skull in dorsal view.

Palatal complex. As judged from a preserved posterior part of the right vomer, this bone was a very broad plate superimposed over the medial maxillary border to produce an incomplete neochoanate type of internal nares (LAKJER 1927), recalling lacertids. It was strongly swollen at the contact with the palatine (pl. 3 : 1b). This place is somewhat roughened as toothed surfaces usually are but no distinct teeth are recognized on it. With its long, furrow-like main palatine surface *Bainguis* recalls both anguids and lacertids differing from both of them by much more retracted position which is a modern platynotan character state. The posterior extent of the pterygoid process of the palatine is unknown. Both the maxillary and vomerine processes extend ventrally to articulate with corresponding bones. The quadrate is a very slender bone with a tympanic crest represented merely by a rudimentary ridge. The medial crest is probably poorly developed too. A very oblique position of the quadrate in both specimens having their jaws in occlusion seems to be natural of *Bainguis* in the resting phase of the jaw apparatus. A small posterior movement of such a long and oblique quadrate should have caused an important increase in height of the posterior, active segment of the quadric-crank mechanism and could have been useful for retraction of the jaw apparatus. However, the frontoparietal suture, which is covered by frontoparietal scutes, affords no indication on the intensity of the skull kinesis.

Occipital segment. The basisphenoid is covered by a thin, flat bone blade overlapping the basioccipital (pl. 3 : 1, fig. 7J). It is interpreted as a parasphenoid. Laterally it reaches up to the tops of the sphenoccipital tubercles and medially almost to the same level. Neither the anterior extent of the parasphenoid nor the shape of the basipterygoid processes are known due to the damage. The position of the tops of the sphenooccipital tubercles, which seems to be very retracted, cannot be precisely determined but only estimated at about 1/4 the length of the brain case base from the top of the occipital condyle. Extending from the ventrolateral part of the condyle towards the posterior part of the sphenoccipital tubercle is a prominent and sharp crest separating a horizontal ventral surface of the brain case from a posterior, concave, subvertical area probably occupied by the rectus capitis anterior and the longissimus cervicis.

Separating the probable surfaces of insertion of the longissimus cervicis and the obliquus capitis, a ridge runs from the upper margin of the occipital foramen towards the posteroventral margin of the paroccipital process. Foramen magnum is large and rounded. The distal extremity of the paroccipital process is a triangle facing ventrally. Its anteroventral margin passes anterodorsally into the prootic crest. Delimited posteriorly by a tuberal crest and anteriorly by a prootic margin is a large and deep fossa containing both the foramen ovale and the occipital recess. The anterior process of the opisthotic separating these foramina lies very deep in this fossa. A very large and open recessus vena jugularis faces ventrolaterally. The prootic crest directly underlies a horizontal semicircular canal. There is no trace of the alar process of the prootic.

Mandible. The mandible is very long and slender. It is provided with a long retroarticular process. A part of its postcoronoid ramus being not preserved, the disposition and size of the mandibular fossa and the extent of the angular are reconstructed from their anterior and posterior parts. A part of the ramus directly adjoining the mandibular articulation extends

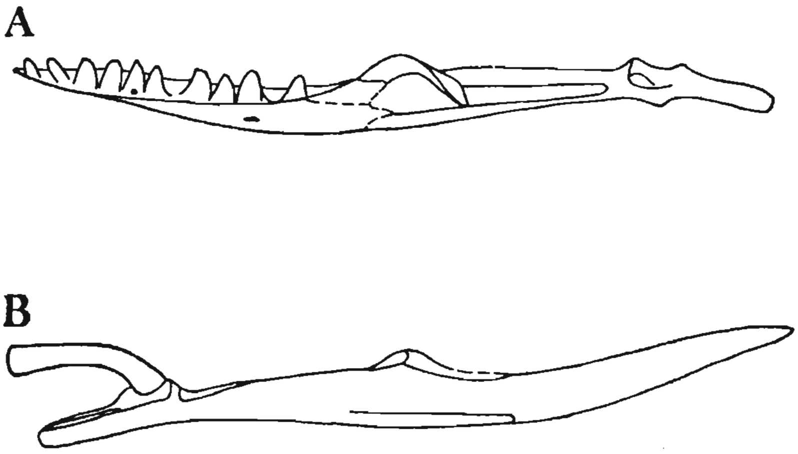


Fig. 6
Bainguis parvus gen. n., sp. n. Mandible. A-Medial view, B-Lateral view.

horizontally medial of this articulation (pl. 3 : 1a), which is difficult to demonstrate in the picture. The coronoid is a very fine bone. As reconstructed from its preserved part it probably extended much anteriad medial of the dentary, this part being overlapped by the splenial. In the lateral aspect the nature of the coronoidodentary contact is not clear. The most probable posterior extent of the splenial is reconstructed from the sp surface of the prearticular (figs 6, 29). Anteriorly, the splenial reaches very far towards the top of the dental. This primitive character state as well as the anterior turning of the splenial to the ventral border of the mandible characteristic of Anguimorpha are quite evident on the specimen ZPAL MgR-II/46. The lack of a subdental ridge and, consequently, of a dental gutter is also beyond any doubt. In contrast to this, the type of tooth replacement is not quite clear.

Dentition. The maxillary teeth are low, broad, conical in shape. They are firmly ankylosed to the maxilla and have no resorption pits. The mandibular teeth are much higher and narrower than the maxillary ones. Their exact shape cannot be determined because of the bad state of preservation.

Infraorder **Anguimorpha** FÜRBRINGER, 1900
Superfamily **Platynota** BAUR, 1890
NECROSAURIAN GRADE

Definition. — Anguimorphan lizards tending to the development of intramandibular mobility, involving a lack of coronoid overlap on dentary, posteriorly shortened splenial as well as a straightening of the posterior margin of dentary. External nares unretracted. Internal nares retracted; palatine shortened. Nasals paired. Osteodermal skull covering tending to multiplication. Parietals fused. Parietal foramen situated posterior to the frontoparietal suture. Oblique pterygopalatine joint. Toothed pterygoids and palatines. Simple dentine folding. Brain case structure derived: extensive alar process, posteriorly narrow recessus vena jugularis, trapezoidal sphenoccipital suture. State of tooth crowns, osteodermal skull covering and body size variable. Tendency to size increase.

Discussion. — The necrosaurian grade is distinguished within the superfamily Platynota to designate some groups of primitive platynotan lizards probably not belonging to the same family but corresponding to the diagnosis of the family Necrosauridae HOFFSTETTER (1943).

The family Necrosauridae has been erected by HOFFSTETTER (1943) to embrace *Varanus*-like lizards from the phosphorites of Quercy (Eocene). FILHOL (1838, 1876, 1877) named them successively *Palaeosaurus cayluxi*, *Necrosaurus cayluxi* and *Palaeovaranus cayluxi*. According to HOFFSTETTER (1943), they all belong to one species for which the name *Necrosaurus cayluxi* is valid. No formal diagnosis of the family has been given by HOFFSTETTER but characteristic features of this family are in agreement with the diagnosis of the genus *Palaeovaranus* FILHOL, 1877 proposed by FEJERVARY (1935). Both authors stress the combination of varanid character states (understood as characters of the mandible, teeth and shape of the parietal) with normally developed nasals and, accordingly, unretracted nares. According to HOFFSTETTER (1943) *Melanosaurus giganteus*, described by KUHN (1940, pl. 4) from Geiseltal (Eocene), belongs to the genus *Necrosaurus* and thus to the family Necrosauridae. Apart from the characters of teeth and parietals conspicuous in the Geiseltal specimen, he based this identification on vertebrae and body osteoscutes. However, the state of external nares which is critical for such an assignment is not known from KUHN's material, nor is it apparent from a new material assigned to this species by HAUBOLD (1977). Some other character states which could be of familial rank, at least in combination with other features, such as the state of subolfactory processes of frontals and the type of squamation are not given, or not clear, for the genus

Necrosaurus and, thus, for the family. Judging by the photograph given by KUHN (1940) as well as by that kindly sent me by HAUBOLD (Geiseltal Museum, Halle), *Necrosaurus giganteus* has an unpaired row of osteodermal units extending over a sagittal suture and is thus much advanced towards a small-plate pattern of osteodermal skull covering. The structure of the brain case which is presumably typical of the Platynota remains unknown.

As shown by the present material, the necrosaurian condition of unretracted nares united with a platynotan mandible and teeth is satisfied not only by the Necrosauridae but also by three new genera which are not likely to belong to the same family and will be further referred to as necrosaurian lizards independently of their familial affinity.

The Necrosauridae are provisionally considered as a waste-basket for the necrosaurian platynotan lizards distinguished by mandibular adductors attached to the lateral parts of parietals, by a determined dentine folding and a disintegrated osteodermal skull covering. Great variability of size and osteodermal skull covering is assumed for this family, which permits the inclusion of the North American genus *Parasaniwa* and thus of the family Parasaniwidae, a solution proposed by ESTES (1983). The representatives of the last named genus are twice as small as those of *Necrosaurus giganteus* and display the osteodermal skull covering much less advanced towards a small-plate pattern than is the case in this species.

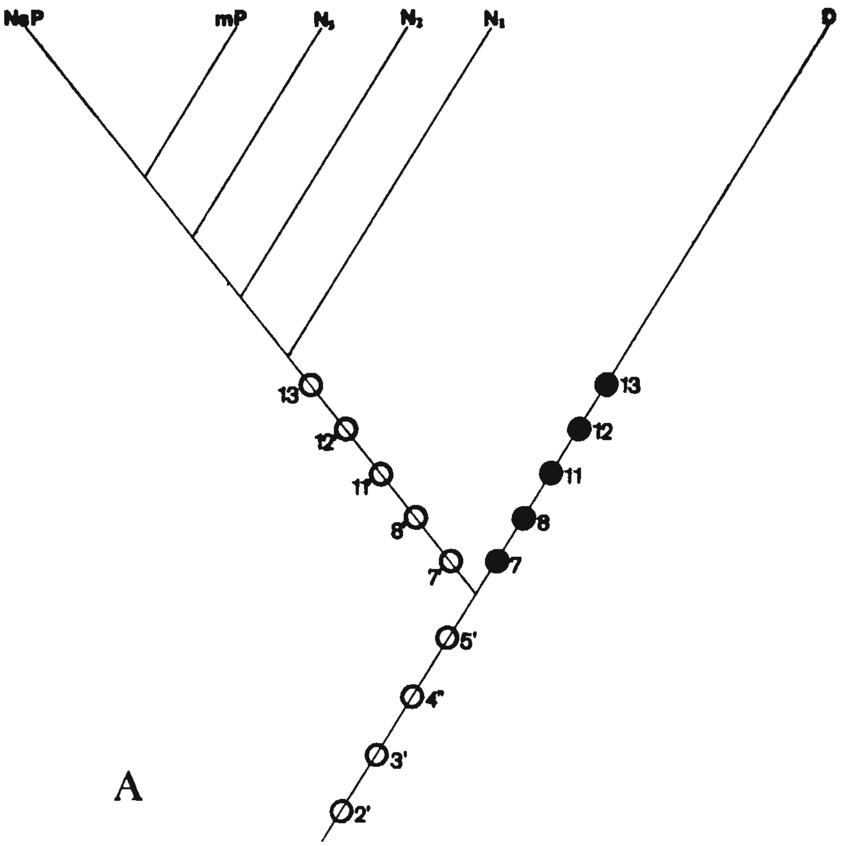
Among the Late Cretaceous Mongolian necrosaurian genera only one, *Praviderma* gen. n. with only one species *P. inexacta* sp. n., a small lizard with a mucronate small-plate skull covering, may be included into the family Necrosauridae. Two other representatives of the Late Cretaceous necrosaurian lizards, *Gobiderma pulchra* gen. et sp. n., and *Proplatynotia longirostrata* gen. et sp. n. do not fit the present diagnosis of the family Necrosauridae and must be put outside the range of this family. The genus *Gobiderma* differs from the Necrosauridae by its mandibular adductors attached to the ventral surface of the parietals and by a strong development of small-plate skull covering with a perforated surface. It recalls *Holoderma* by both these character states, while differing from this genus in overall adaptation of the maxillary segment of skull (preserved supratemporal arch, no contact between prefrontal and postfrontal above the orbit). Taking into account the uniformity of the adaptive character of the maxillary unit within the range of lizard family, as exemplified by the Anguidae or the Lacertidae, I believe that the difference between *Gobiderma* and the Necrosauridae in the disposition of the mandibular adductors is of a familiar or, at least, subfamilial rank. However, it should be kept in mind that some genera, such as *Varanus* (see MERTENS 1942) display an increased variability of this character state which has, thus, only a specific value. Therefore, I prefer to leave the genus *Gobiderma* within the informal taxonomic group, the necrosaurian grade, without any familial assignment, until new data concerning the variability ranges of the included taxa permit the reconstruction of the internal taxonomic structure of this group.

The same solution seems also advisable for the third necrosaurian representative of the Late Cretaceous Mongolian fauna, *Proplatynotia longirostrata* gen. et sp. n. *Proplatynotia* differs from both the Necrosauridae and *Gobiderma* by two characters. These are a lack of basal fluting of teeth and a primitive structure of the brain case (see pp. 34, 35). However, the latter character may not be quite securely relied upon because of the bad preservation of the brain case. If it is really primitive, it would indicate that the ancestor shared by *Proplatynotia* and

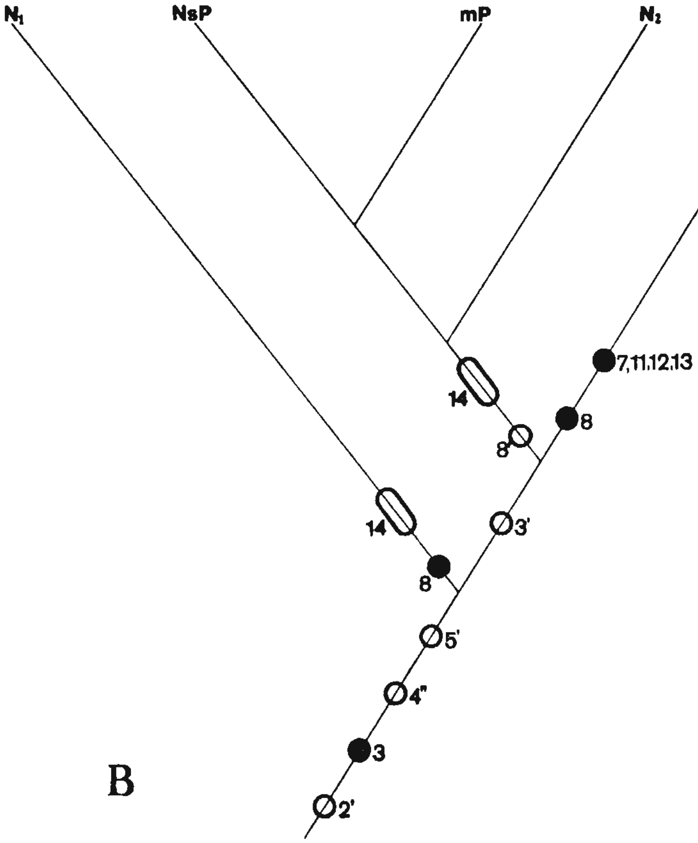
→

Fig. 7

Cladograms illustrating two hypotheses of the origin of necrosaurian lizards. A-Monophyletic origin, B-Polyphyletic origin. Necrosaurian stem of the Platynota (NaP); modern platynotans (mP); Diploglossa (D); necrosaurian families (N_1, N_2, N_3). Numbered circles denote character states. *2'* state of splenial, *3'* state of brain case, *4''* state of sphenoccipital suture, *5'* state of mesokinetic articulation, *7'* state of size increase, *8'* state of complication of dentine folding, *11'* tendency to formation of intramandibular joint, *12'* tendency to multiplication of the skull covering, *13* tendency to retraction of internal nares, *14* state of predatory adaptation equivalent to character states *7'*, *11'*, *12'* and *13*. For detailed explanations to character states *2-9* see fig. 1.


NsP
mP
N_3
N_2
N_1
D
13'
12'
11'
8'
7'
13
12
11
8
7
5'
4"
3'
2'

A


N_1
NsP
mP
N_2
D
7,11,12,13
14
8'
8
14
3'
8
5'
4"
3
2'

B

Anguimorpha *sensu stricto* (Diploglossa and Platynota) is more remote in time than the common ancestry these superfamilies share with one another, assuming that the derived character states of the brain case are synapomorphic in these superfamilies (pp. 20 and 67). The lack of the basal fluting in *Proplatynotia* tends to support this suggestion. Since, according to RIEPPEL (1978) the varanid tooth replacement is correlated with the development of plicidentine in the Platynota, the even surfaces of the teeth in *Proplatynotia* point to nonplatynotan relationships of this genus. Although the overall appearance of the maxillary segment of skull of *Proplatynotia longirostrata*, its sculpture and its mandible strongly suggest the platynotan affinity, its independent origin from the anguimorphan stem and, consequently, a polyphyletic nature of the group of necrosaurian lizards, cannot be entirely ruled out.

The problem of the polyphyletic versus monophyletic nature of the necrosaurian group of lizards may be studied with the assistance of cladistic methods in the following way.

Documented by at least four shared derived character states: a shortened splenial (2'), a straight frontoparietal suture (5') and the states connected with a modernization of the brain case, numbered 3', 4' (see figs 1, 7), the monophyly of the main anguimorphan stem (Anguimorpha *sensu stricto* = Diploglossa+Platynota) seems well demonstrated. This, however, does not unequivocally imply the monophyly of the whole necrosaurian group.

The monophyly of the necrosaurian group is strongly endorsed by a set of derived character states, the necrosaurian lizards share with each other but not with the Diploglossa. These are tendencies: to size increase (7'), to multiplication of the skull covering (12'), to retraction of internal nares (13) and to formation of the intramandibular joint (11).

The hypothesis (fig. 7B) that, at least, one of the necrosaurian taxa (the genus *Proplatynotia*) has been derived, independently of the true platynotans, from a diversified ancestral anguimorphan group, seems much less convincing than the monophyletic hypothesis (fig. 7A), but it cannot be entirely rejected. It may be postulated that the development of character states 7', 11, 12', 13 may be reduced to a single step (14) forward on the way to predatory adaptation which consisted in the improvement of the skull kinesis and the increase of size variability (usually size increase). The improved skull kinesis probably involved a shortening of palatines (equal to retraction of internal nares, see p. 84). Connected with the predatory adaptation was also gradual development of the intramandibular mobility (11') with all corresponding changes of bone disposition described by MCDOWELL and BOGERT (1954). The tendency to size increase (7') could influence the osteodermal skull covering (12). Such a simple step could occur more than once and could produce similar character states which should be regarded as a result of parallelism (fig. 7B).

Although the problem is not definitively solved I would rather accept the monophyly of the necrosaurian group. *Proplatynotia* will be thus included into the Platynota but its assignment to a family seems premature.

Family *uncertain*
Genus *Proplatynotia* nov.

Type species: *Proplatynotia longirostratia* sp. n.
Derivation of the name: Lat, *pro* — before, the most primitive of platynotans.

Diagnosis. — Medium-sized platynotan lizards, about 4 cm in skull length. Sharp dentition without basal fluting. External nares not retracted to separate maxilla and nasal. Nasals paired. Subolfactory processes developed. Postorbital joined to postfrontal from lateral side, broadly entering into the orbit. Alar processes lacking or small. Premaxillary foramina well developed. Adductor musculature originating lateral on the parietal. Small-plate osteodermal covering.

Stratigraphical and geographical range. — Known only from the type horizon and type locality.

Proplatynotia longirostrata sp. n.

(pls. 4 : 2, 5; 5 : 1, 2; 7 : 4; 13 : 4, figs. 4B 8, 9A)

Holotype: A skull with a mandible ZPAL MgR-I/68.

Type horizon: Upper Cretaceous, ?middle Campanian, Barun Goyot Formation.

Type locality: Khulsan, Nemegt Basin, Mongolian People's Republic.

Derivation of the name: Lat. *longus* — long, *rostrum* — a snout, longirostrata because of the elongate rostral part of the skull.

Diagnosis. — Skull long and slender without any strong expansion of jugal arches. External nares slightly elongated at the cost of anterior part of the snout. Very long nasal process of the premaxilla entering a short distance between the nasals. Number of tooth positions is 15 on maxilla, about 3 on a half of the premaxilla and 16 on dentary. Osteoderms lacking from the skull at least. Osteodermal skull covering consisting of rounded thickenings of bone surface.

Material. — The only specimen ZPAL MgR-I/68, the holotype, is a posteriorly damaged skull with a mandible. The almost complete right half of the mandible lacks only a retroarticular process, whereas the left one is fragmentary. The occipital part of the brain case and supratemporal arches are lacking except for the anterior part of the right one.

Measurements. — See Tables 2 and 3.

Discription. — **Skull as a whole.** The skull is long and slender, slightly tapering from the postorbital region forwards. The ratio: maximum width of the skull, over a posterior part of the orbital region, to the width of the premaxillary rostral body is about 3.7. The elongated appearance of the preorbital part is mainly the result of the lengthening of both the maxillary and premaxillary bordering of the external nares. Although posteriorly extended, the external nares do not wedge in between the nasals and the maxillae. The dorsal surface of the parietal is divided into a medial part and narrow lateral parts destined for the origin of the mandibular adductors. The osteodermal skull incrustation of small-plate type is confined to the regions tightly connected with the skin.

Skull roof. The premaxilla has a rather broad semilunar rostral body. Paired palatine processes are separated from each other by a shallow, angular, posterior notch and from the maxillary process by broad, shallow, semicircular notches contributing to borderings of big and rounded premaxillary foramina. Paired incisive processes project from the ventral surface of the palatine processes. The maxillary process is dorsally overlapped by a narrow finger-like process of the maxilla. Nasal process of the premaxilla is very long, lanceolate in outline and triangular in transverse section, the apex of the triangle being directed ventrad. Its course is horizontal almost all over its length owing to the rostral part of the skull being very flat. In its posterior part there is a trace of a sagittal suture. The septomaxilla is an elongated capsule dorsally flattened. Its posteromedial corner extends much more posteriad than does the posterolateral.

The nasals are paired. They are roughly triangular, elongated bones, their very anterior parts (overlapped by the nasal process of premaxilla) excluded. Superficially they are separated from each other by short processes of the frontals and premaxillae. The nasomaxillary suture extends subparallel to the sagittal axis. The surface of the nasal is roughened by flat osteodermal incrustations which are irregular but not asymmetrical.

The frontals are paired with straight, parallel lateral margins diverging posteriorly. Their anterolateral processes contact the maxilla. The frontoparietal suture is straight and rather loose. The minimum width of the frontal is about 1/3 of their posterior broadening. The extensive subolfactory processes are broadly separated from each other ventrally. They attenuate posteriorly and disappear in the broadened part of the frontals about 1/3 their length from their rear.

The orbital borders of the frontal are thickened and segmented. Posteriorly this segmentation turns into a small-plate osteodermal covering, the surface of osteodermal units being sculptured with pits and furrows. Between the thickened and fragmented orbital borders there remains just a very narrow surface which is also subject to segmentation, the rounded osteodermal swellings being situated on the sagittal suture (see figs 4J, 1B). Remaining between the thickened borders and the frontoparietal suture is a small tringular surface also covered with small-plate incrustation.

The entire length of the parietal with its posterolateral processes included is about 0.7 of the length of the frontal, the main body of the parietal being most of this. The posterolateral extensions were probably very short, the unpreserved part being considered insignificant. The posterior border of the parietal presents a broad and shallow concavity. The dorsal surface of the parietal is broad and flat. It is bordered by laterally concave external parietal crests and posteriorly concave nuchal crest. These crests do not fuse with each other before entering deep onto the posterolateral extensions of the parietal. As a result the posterolateral extensions have flat dorsal surfaces. Destined for the mandibular adductors, lateral surfaces of the parietal continuous with the lateral surfaces of the posterolateral extensions, face dorsolaterally. The medial surface of the posterolateral extension is very low, almost none, but produces a horizontal lamina comparable to, but more lateral than that present in *Anguis*. The maximum width of the parietal at the frontoparietal suture is about 4/3 of its sagittal length. The parietal foramen is situated about 1/3 of the length of the parietal from the frontoparietal suture. The same small-plate osteodermal incrustation as that on the frontals is present on the parietal except for the posterior 1/3 of their length and their lateral parts.

The maxilla has a long nasal process bending to the dorsal surface of the skull to contact the nasals. Posteriorly it is sutured to the prefrontal, the suture being posteriorly concave. Extending medially to reach the palatal processes of the premaxilla are medial processes of the maxillae. Each of them bears a sharp crest on its dorsal surface separating its anterior and posterior surfaces sloping in the opposite directions. Posterolateral to this crest is an anterior inferior alveolar foramen. The palatal surfaces of these processes are the only broadened parts of the palatal shelf. These contribute to the lateral bordering of the fenestra vomeronasalis externa (aperture of the Jacobson's organ of the neochoanate type). The palatomaxillary suture is very long (almost 1/3 the length of the palatal shelf) and almost parallel to the jaw axis, there being only a slight bending of the medial margin of the maxilla at the beginning of the palatal contact. The suture is very loose. Maxilla extends anterior of the palatal shelf by means of a narrow process overlapping the premaxilla and bordering the premaxillary foramen from lateral. It also extends posteriorly to underlie an anterior part of the orbit. The fenestra exochoanalis is long and narrow.

A subtriangular dorsal surface of the prefrontal extends into a long and narrow supraorbital process reaching to a half of the frontal length and broadly separated from the postfrontal. It has a thickened and protrudent orbital border. This border along with a sculpturing of three rounded osteodermal thickenings makes an impressive point of similarity with *Gobiderma* (see p. 43 and fig. 11), but is presumed to result from the similarity of the incrustation process only. The orbital lamina of the prefrontals sutures medially to the subolfactory process of the frontal and ventrally to the palatine, by a transverse suture. Its lateral side sutures to the lacrimal and contributes to the bordering of the lacrimal foramen.

The lacrimal is a thin plate-like bone with a concave lateral surface. Its orbital margin is superimposed by a spine probably of the osteodermal character. Its suture with the jugal is not clear. The jugal extends in a parasagittal plane. It has a deep subhorizontal ramus with its lateral surface concave and roughened, a distinct jugal process and a slender smooth ascending process making up a sliding joint with a postorbital. The dorsal margin of the jugal is concave. Medially it contacts with the ectopterygoid which probably separated both the jugal and the maxilla from the suborbital fenestra.

The postfrontal is a V-shaped bone, its long anterior and posterior processes being pressed

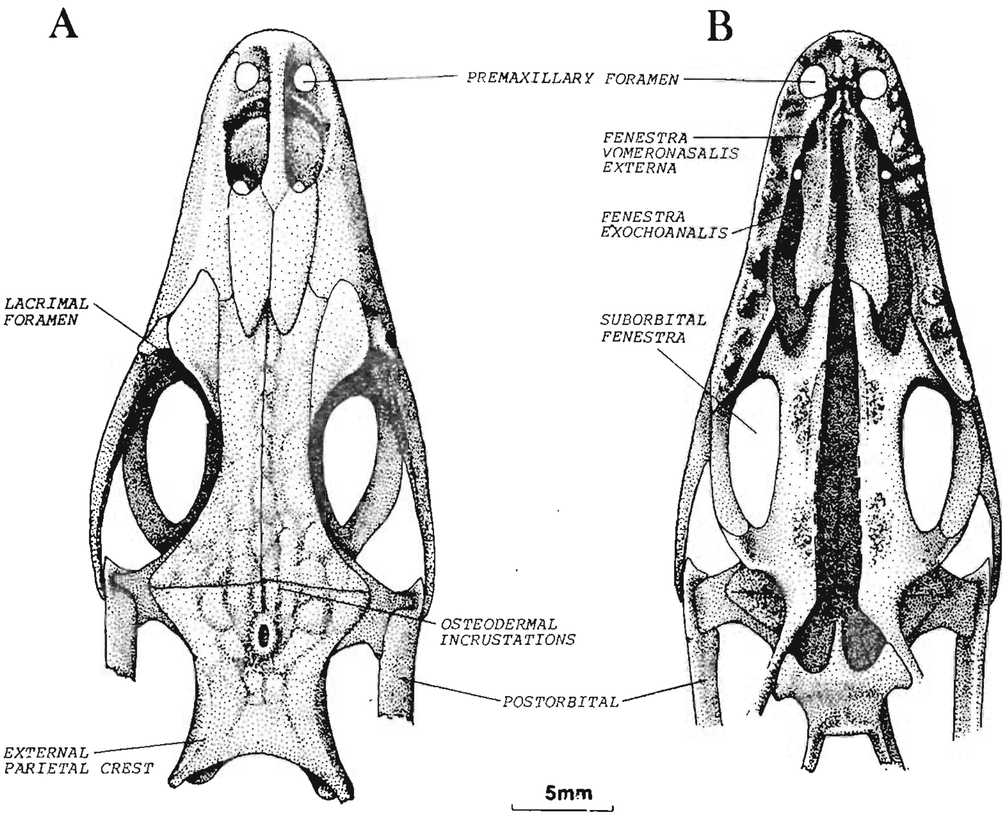


Fig. 8
Proplatynotia longirostrata gen. n., sp. n.; Skull. A-Dorsal view; B-Ventral view.

into the margins of the frontal and the parietal, respectively. Its distal angle is overlapped and superficially subdivided by the postorbital (see fig. 8). The postorbital is a very strong bone with a dorsoventrally flattened shaft. It extends posteriad in an oblique plane, so that its dorsal surface faces dorsolaterally instead of dorsally. The anterior part is much thickened relative to the remaining bone because of its diverse functions; medially it overlaps the postfrontal, while extending laterally to reach the jugal and anteriorly to contribute an important part to the orbital border. Aparat from its ventral surface joining the postfrontal, this part has three surfaces: the external dorsolateral surface, the ventrolateral, jugal surface and anterior orbital surface, exactly as is the case in *Paravaranus.* This is probably a primitive structure of the postorbital region.

Palatal complex. The vomers are broad bone blades closely apposited to each other medially but not fused. The parasagittal region is concave in ventral view which is the only visible aspect. One of two foramina situated above the midlength of this concavity is to be regarded as a vomerine foramen for a medial palatine ramus of the facial nerve. The general shape of the vomer is convex in a transverse section, while flattening posteriorly. The posterior part extends laterally to diminish the fenestra exochoanalis. The anterior part of the vomer is directly comparable to that of the Anguidae, especially to those having a premaxillary foramen, but it is more differentiated into furrows and ridges and has more elongated anterior processes in *Proplatynotia.* This is connected with the elongation of the snout which is not accompanied by the elongation of the palatal processes of the premaxilla, as characteristic of *Varanus.* Extending from the top of the anterior process along the surface of the vomer to about half its length is a protrudent ridge. Medial to the anterior process and posterior to its base is a medial process of the vomer contacting with its fellow of the other side and separated from the anterior process by a con-

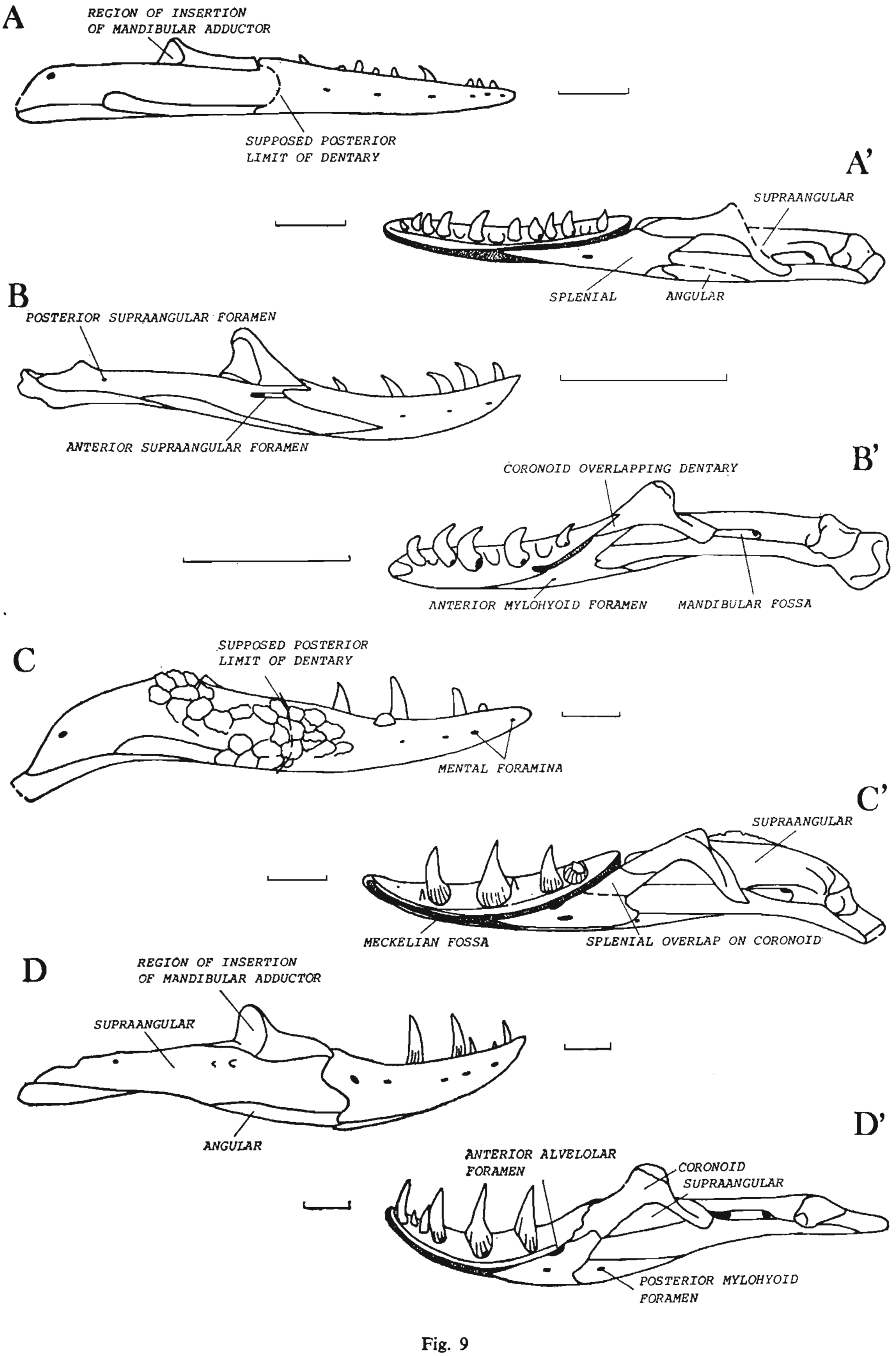
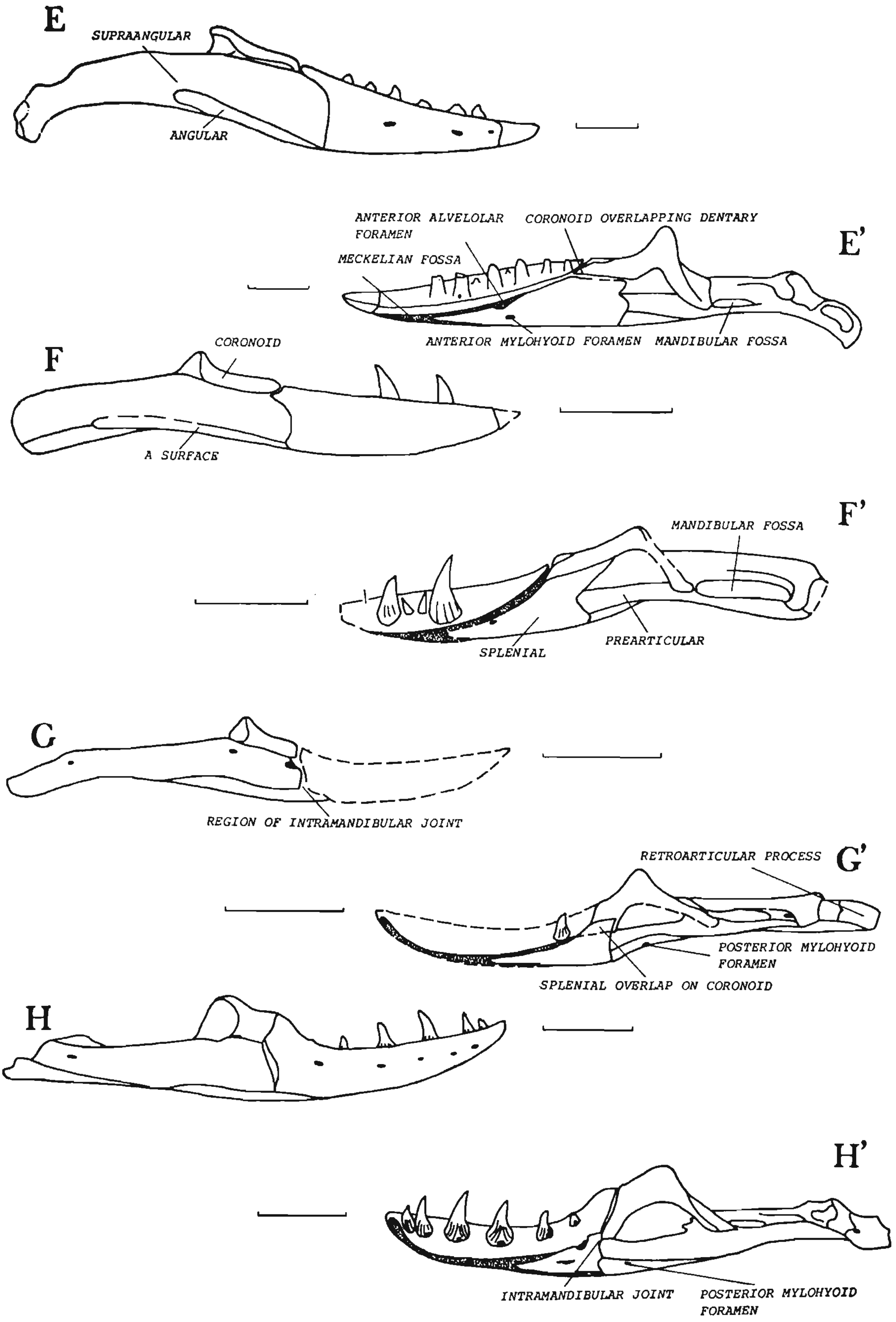


Fig. 9

Mandibles in Anguimorpha. A — *Proplatynotia longirostrata* ZPAL MgR-I/68; B — *Anguis fragilis* ZPAL z. p. R-I/5; C — *Gobiderma pulchra* ZPAL MgR-I/64; D — *Heloderma* sp. ZPAL MgR-I/4; E — *Saniwides mongoliensis* ZPAL



MgR-I/72; F — *Parviderma inexacta* ZPAL MgR-I/43; G — *Cherminotus longifrons* ZPAL MgR-III/67, reconstructed; H — *Lanthanotus borneensis* MCZ 8305. Lateral aspects left; Medial aspects right. Scale 10 mm.

cavity. The lateral margin of the vomer is produced towards the palatal shelf of the maxilla anterior and posterior of the fenestra vomeronasalis in a neochoanate or incomplete neochoanate manner. Posterior to this fenestra and parallel to its border a concave lacrimal groove is very distinct.

The palatine has a long vomerine process contacting with the vomer only posteromedially, the posterolateral part of the vomer extending loosely to the choana. The vomeropalatine joint is anterior to the palatomaxillary suture. The maxillary process is short at the base but twice as long at the palatomaxillary joint. The articular part has a long longitudinal furrow for the maxillary border. It is roofed dorsally and open ventrally and indicates the important amount of mobility of this joint. The choanae are very retracted in a way characteristic of advanced Platynota. This is discordant with the state of the external nares which remain at the necrosaurian evolationary level. The retraction of the choanae is, thus, not likely to be a result of the posterior shifting of the external nares. It is expressed by a shortness and a vertical position of the lamina connecting both anterior processes of the palatine. The pterygoid process of the palatine is a broad and long lamina bearing teeth, provided with a medial bone shelf, very smooth and situated deep to the palatal level in a ventral aspect. This shelf, which is a place of a pterygopalatine contact, is suggestive of the occurrence of shift movements in this joint. The pterygopalatine suture is not clear.

The palatine process of the pterygoid produces a triangular bone blade bearing small palatal teeth and narrowing anteriad. The quadrate process which is, as usual, a long plate of bone medially concave running posteriad in a vertical plane, is separated from the palatine process by a distinct bend. The basipterygoid joint is bordered ventrally by an angular projection preventing from a disarticulation of the joint. It passes into a sharp ventral part of the quadrate process. The ectopterygoid is a long, only slightly curved bone bordering the suborbital fenestra from lateral. A slight ventral projection of this bone directly adjoining the pterygoectopterygoid articulation is the only trace of the pterygomandibularis origin. The epipterygoid is missing from the specimen.

Occipital segment. The basisphenoid+parasphenoid is preserved. The fusion of both parts of the sphenoid region can be traced on the left side of the specimen in posterior view (pl. 4 : 5b). The parasphenoid produced sharp ventrolateral crests and probably made posterolateral extensions, now broken off. It contributes to the posteroventral surface of the basipterygoid process but its share in the dorsal surface of this process is not clear. The posterior border of the sphenoid part provided with two condyles is produced by the basisphenoid. This posterior border is straight and transverse, so as to separate the posterolateral extensions of the parasphenoid. If they existed, which was obviously the case, they would produce a trapezoidal type of sphenoccipital suture. The basipterygoid processes extend laterally and slightly anteriorly in an almost horizontal plane. Their articular ends are much broadened. The preserved parts of the prootic show no traces of the alar process, anterior to the anterior semicircular canal. But they do not exclude its existence anterodorsal to this canal, this border being damaged. Running just below the horizontal semicircular canal a sharp, protrudent prootic crest overhangs a deep, but not narrow, recessus vena jugularis.

Mandible. The shape of the coronoid, its very loose contact with the dentary and the general shape of the dentary are exactly the same as the corresponding features in Gobiderma and Parviderma, but the lower border of the mandible is quite straight, there being no sigmoid curvature at all.

The dentary is very low and long. Its maximum height to length ratio is 2/9. The Meckelian fossa is correspondingly very long and low, and becomes ventral anteriorly. The tooth-bearing border is swollen beneath the tooth-bases and mainly so in the anterior half of the dentary, while fading posteriorly. The posterolateral border of the dentary is nearly vertical and sligthly concave, as reconstructed from the both halves of the mandibles of ZPAL MgR-I/68.

The splenial reaches posteriorly more than half the length of the anterior ramus of the coronoid and anteriorly to about half the length of the dentary. The small, oval anterior mylohoid foramen is situated beneath the third tooth position from the rear. Both the dentary and the splenial are involved in formation of the anterior inferior alveolar foramen. The anterior ramus of the coronoid is elongated, horizontal and bifurcated at its anterior end. It is not beveled from the main plane of the mandible. Its medial part is developed deep to the splenial but its exact extension is unknown. The dorsally projecting apex being damaged, only its general direction to the anterior border of the mandibular fossa is known. The dorsal border of the supraangular is rather thick and rounded behind the coronoid. It projects but a little medially to contribute to the glenoid. The mandibular fossa does not reach the glenoid region. The suture between the prearticular and the surangular is quite typical. The extension of the angular is not quite clear; it is reconstruced in fig. 9A.

Dentition. The number of tooth positions is about 6 on the premaxillary, about 15 on the maxilla and about 16 on the dentary. The number of teeth on the maxilla and on the dentary is 12 and about 10 respectively. The teeth are very widely spaced even if not separated by spaces for successive teeth. They are very *Anguis*-like, only slightly less posteriorly curved than is the case in this genus. There is no basal fluting. The method of replacement is clearly varanid. No basal foramina have been observed on teeth.

Family **Necrosauridae** HOFFSTETTER 1943 (faute de mieux)

Genus *Parviderma* nov.

Type species: *Parviderma inexacta* sp. n.

Derivation of the name: Lat. *parvus* = small; the word derma included to the name should indicate a similar systematic position as that of *Gobiderma* gen. n.

Diagnosis. — Small necrosaurid lizards with very narrowed and fused frontals. Subolfactory porocesses of frontals rudimentary. Osteodermal skull incrustation of small-plate pattern. Palpebral bone present. Postfrontal of quadrangular type. Palatine and frontals toothed. About 7—8 tooth positions on the dentary.

Stratigraphical and geographical range. — Known only from the type horizon and type locality.

Discussion. — The genus *Parviderma* nov. differs very much from *Necrosaurus* by its very narrow, fused frontals, strong, tuberculate osteodermal skull incrustation (as in *Xenosaurus*) and small size. Although the only specimen representing the genus is probably a young animal, the character of frontals is not likely to be much changed in the ontogenesis. Other differences could tend to diminish with age but are too distinct to disappear. A weak development of the subolfactory processes of the frontals is supposed to be another difference if their state would be known in *Necrosaurus*, which is not the case. This could have resulted from a stratigraphic age difference. In spite of these stated and presumed differences, the genus is included into the family Necrosauridae as being a necrosaurian lizards having lateral mandibular adductors. The differences are regarded as generic, until new evidence comes.

Parviderma inexacta sp. n.

(pls. 5 : 3, 4; 6 : 5, figs. 9P, 10)

Holotype: A fragmentary skull with mandible ZPAL MgR-I/43.

Type horizon: Upper Cretaceous, ?middle Campanian, Barun Goyot Formation.

Type locality: Khulsan, Nemegt Basin, Mongolian People's Republic.

Derivation of the name: Lat. *in* — negative particle, *exactus* — exact. *Inexacta* means: assigned to a family but not exactly fitting into it.

Table 2

Dimensions of skulls of *Proplatynotia longirostrata, Parviderma inexacta and Gobiderma pulchra* in mm

Species and ZPAL cat. nos.	*Proplatynotia longirostrata* MgR-I/68	*Parviderma inexacta*		*Gobiderma pulchra*		
		MgR-I/43	MgR-III/64	MgR-III/65	MgR-III/66	MgR-I/54
Skull as a whole						
Condylobasal length	—	—	50	—	—	—
Total length	—	—	52	—	e. 34	—
Length of posterior skull unit (or maximum parietal length)	>10	—	19.5	e. 22.5	12	—
Length of snout unit	27	—	32.5	—	—	—
Length of external nares	7.5	—	8.5	—	—	—
Maximum width over premaxillary	4	—	7	—	—	—
Maximum width over jugal arches	ca. 15	—	ca. 23	—	—	—
Width of postorbital region	16	—	20	ca. 27	14	—
Maximum overall width	—	—	ca. 35	ca. 36	22	—
Posterior depth	—	—	10	—	—	—
Depth anterior to orbits	4	—	5.7	—	3	—
Frontals						
Sagittal length	13	10.5	17.5	—	12	—
Anterior width	5.8	3.2	5.3	ca. 7.5	3	4.6
Posterior width	12	7.3	14.2	ca. 24	10	—
Minimum width (about the middle)	4.2	2	5.4	9	3.6	5.2
Parietals						
Sagittal length	8.2	—	14.5	ca. 15.2	10	—
Maximum length	—	—	17	ca. 20	12	—
Minimum width	7	—	9.8	ca. 15.5	7	—
Minimum distance between external parietal crests	6	e. 3.5	9.8	ca. 15.5	7	—
Maximum posterior width	—	—	18.6	ca. 28	12.1	—
Brain case						
Posterior depth (metakinetic joint to central surface of the occipital condyle)	—	—	6.3	ca. 9	—	—
Distance between paroccipital processes	—	—	22.5	ca. 22	—	—
Length in ventral aspect (occipital condyle to the basis of anterior parasphenoid process)	—	—	11.5	ca. 14	—	—
Vomer						
Maximum length	11.9	—	11	—	e.10	—
Maximum width	2	—	2.2	—	2	—
Quadrate						
Length of shaft	—	—	11	—	8	—
Width of distal condyle	—	—	—	—	—	—

Diagnosis. — The genus is monotypic. See the diagnosis of the genus.

Material. — ZPAL MgR-I/43, the holotype, is the only known specimen. It is a strongly damaged skull with the left mandible. A whole anterior and anteroventral part of the snout (premaxilla, vomers, most of maxillae), the jugal and supratemporal arches as well as the posterior part of the skull (posterior half of parietal, occipital and otic parts of the brain case) are wanting. The mandible is deprived of its anterior part as well as of a ventral margin of the dentary. Only one upper tooth and two lower teeth are preserved.

Measurements. — See Tables 2 and 3.

Description. — **Skull as a whole.** Judging by the preserved parts, the skull is characterized by very large orbits separated by narrow frontals. Based on the preserved part of the maxillary border, the external nares are retracted but do not separate the nasals and the maxillae. The origins of the mandibular adductors are dorsolateral of the parietal. Frontals and parietals have a small-plate skull covering with a tubercular sculpture.

Skull roof. Nasals are reconstructed (fig. 10), from their remains, as subtriangular plates contacting the maxilla with their posterolateral sides. They are separated by long and narrow nasal process of the premaxilla and posteriorly by a long and narrow triangular process of the frontals. These processes almost touch one another. The nasal processes of the frontals bear a rounded osteodermal incrustation. The frontonasal suture is W-shaped because of long and narrow processes of the frontals entering between the prefrontals and nasals almost to reach the maxillae. The strongest constriction of the fused frontals is about the middle of their length, the bones getting wider both anteriad and posteriad. The posterior broadening is much stronger than the anterior one, its ratio to the least frontal breadth being 4 : 1, whereas the ratio: anterior breadth to the least breadth is only about 2 : 1. The subolfactory processes of the frontals are low ridges getting a little deeper towards the orbital processes of the prefrontal.

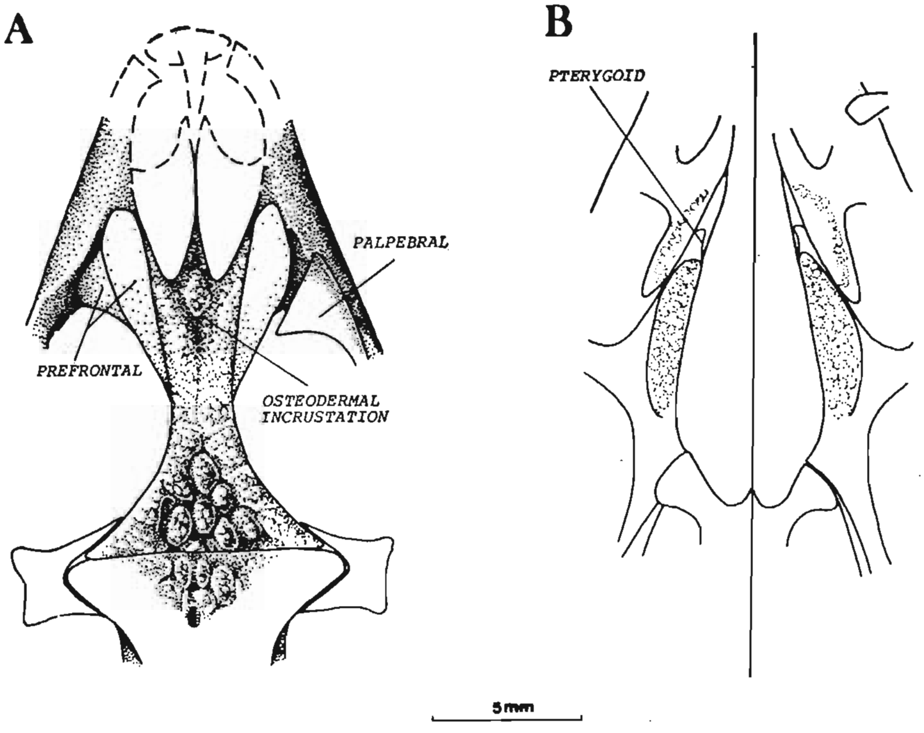


Fig. 10
Parviderma inexacta gen. n., sp. n. Preserved parts of skull of ZPAL MgR-I/43. A — dorsal view; B — Ventral view.

The sculpture of the frontals (figs. 27H, 10A; pl. 6 : 5) consists of bone thickenings, in continuity with the frontal bone tissue, the shape of ridges and tubercles arranged in small-plate pattern. In the anterior part of the frontals, bordered by two prefrontals, this sculpture is quite similar to that present on the frontals of young *Gerrhonotus* (fig. 27B, H, pl. 6 : 5, 7) although the latter represent a large-plate type of squamation. Posterior to the prefrontals, in a region of direct lateral contact with a skin not underlain by skull bones, the osteodermal covering is subject to segmentation which is presumed to result from the influence of this skin. Owing to the constriction of the frontals two segmentation zones meet in a sagittal axis thus leaving no space for a large-scute formation. In the region of the frontal broadening, the segmentation zones diverge to leave a small triangular space. In such a small area the remnants of a large scute pattern have to contract up to the small-plate dimensions. The posterolateral corners of the frontals are bare of ornamentation. The parietal is constricted about the middle of its supposed length. Sharp external parietal crests border lateral parts of parietal destined for mandibular adductors. These surfaces face almost directly lateral. A parietal foramen is much anterior to the supposed half of the parietal length. The maxilla did not probably extend below the orbit. The palatal shelf is very narrow. The prefrontal is a large bone reaching less than half the length of the frontals. Its dorsal surface is very narrow and well separated from the orbital lamina by a sharp crest. The palpebral is a triangular plate of bone with a concave posterior margin. It fits the sharp lateral margin of the prefrontal. The postfrontal has a quadrangular body and two long and slender processes fitted to the frontal and the parietal. Between these processes is the articular facet most of which is occupied by the parietals. A lateral border of the bone produces an articular surface facing a little bit ventrally and posteriorly. This posterior inclination suggest its contact with a laterally situated postorbital rather than with a jugal.

Palatal complex. The palatine has a vomerine and a maxillary process well separated from one another by a strongly retracted choana. The vomerine process reaches more anterior than the palatomaxillary joint. The pterygoid process is very long and slender, with a toothed surface. It offers an articular surface for the pterygoid that is almost parallel to a sagittal axis and has a form of a medial shelf (?hemipterygoid). Being quite smooth and ventrally overlapped by the pterygoid, which is to be seen on the right side (pl. 13 : 2a, fig. 10), it is suggestive of sliding mobility of this joint. The posterior half of the palatine process of the pterygoid is broader than the anterior one and covered with teeth. Posterolateral to it is a triangular, ventrally concave transverse process. Its posterolateral border is produced ventrally for the origin of the pterygomandibularis. Anterior to the basipterygoid joint the pterygoid is produced into a much protruding angular part underlaying the joint. This makes an impression (see pl. 5 : 3) of a strong bent of the pterygoid but the quadrate process extends almost in one line with the medial border of the palatine process in fact. Two basipterygoid processes with rather long and slender stalks extend laterally and much anteriorly.

Mandible. The mandible of *Parviderma* is exactly the same type as that of *Gobiderma.* The similarities consist in the shape of the coronoid, its contact with the dentary and the shape of the dentary, the tooth bearing margin included. The differences are as follows: a much smaller amount of sigmoid curving in *Parviderma*, a lack of a medial leaning of the coronoid from the plane of the mandible and a much lower postcoronoid ramus in *Parviderma* than is the case in *Gobiderma.* The posterior margin of the dentary is damaged but is presumed to be gently concave instead of being deeply incised, and almost vertical. It is situated about the level of the anterior end of the coronoid and the contact between these bones is very loose. However, a strong inflection (fig. 29, d surface) of the supraangular just below the anterior end of the coronoid suggests that the dentary extended to this space and so a slight coronoid overlap on the dentary occurred.

The splenial reaches posterior to about 2/3 the length of the elongated anterior ramus of the coronoid. The exact course of the posterior margin is not known. The anterior extension of the splenial is not known owing to damage but a rapid anterior decrease of its height suggests that it hardly reached half the length of the dentary. Only the anterior ramus of the coronoid is preserved but the posterior one can readily be reconstructed from its traces left at the medial surface of the supraangular and the prearticular. It must have extended nearly to the ventral border of the mandible along an oblique crest extending over the medial surface of the supraangular posteroventrally from the apex of the coronoid. The anterior ramus of the coronoid is elongated, almost horizontal and bifurcated at the anterior end. Its medial part is overlapped by the splenial, its ventral extension being not known. The mandibular fossa is rather low and deeply excavated. The tooth bearing margin is broad and oblique. There is no subdental ridge.

Dentition. The teeth are cone-shaped, broad at the base. Their lower parts have a distinct basal fluting. Each lower tooth has a basal foramen. Behind the anterior of the preserved two lower teeth is a small successive tooth. In the anterior, more vertical part of the tooth bearing border of the dentary the tooth crowns are surrounded by bone tissue and particularly so at their proximal sides. This is less distinct posteriorly with the dental border getting more oblique.

Family *uncertain*
Genus *Gobiderma* nov.

Type species: *Gobiderma pulchra* sp. n.
Derivation of the name: *Heloderma*-like lizard from the Gobi Desert.

Diagnosis. — Medium-sized platynotan lizards about 5 cm of skull length. Sharp dentition with basal fluting. Lower teeth bigger than the upper ones. External nares slightly retracted but not separating maxilla and nasal. Nasals paired. Subolfactory processes developed but weak. Postorbital joined to postfrontal from ventrolateral entering into the orbit. Parietal extended both laterally and posteriorly. Adductor musculature originating ventral on the parietal. Large alar process extending anteriorly. Small-plate osteodermal skull covering very strong, variable in ontogenesis with a tendency to eventually fuse into continuous although superficially sculptured layer. Rounded, perforated osteoderms of *Heloderma* type completely covering cheek region, supratemporal fossa and dorsal surface of the orbit.

Stratigraphical and geographical range. — Mongolian People's Republic, Gobi Desert, Nemegt Valley, Khulsan and Khermeen Tsav II; ?middle Campanian, Barun Goyot Formation and red beds of Khermeen Tsav.

Discussion. — The *Gobiderma* show striking similarities to the Helodermatidae as regards the size, pattern of osteodermal skull covering, shape of teeth and mandible with its characteristic curvature (fig. 9C, D) as well as the mandibular adductors situated ventrally on the parietal. They differ from one another by some character states of evolutionary grade, such as the states of external nares, of subolfactory processes and of the complication of dentine folding. However, *Gobiderma* shows no trace of a helodermoid type of specialization of the skull maxillary segment and, thus, represents more likely an Asiatic substitute of the American group than a group ancestral to the Helodermatidae.

Gobiderma pulchra sp. n.
(pls. 4 : 3; 6 : 1—4; 7 : 1—3; 10 : 2; 13 : 3, figs. 4D, 9C, 11)

Holotype: A skull with a mandible ZPAL MgR-III/64.
Type horizon: Upper Cretaceous, ?middle Campanian, red beds of Khermeen Tsav.
Type locality: Khermeen Tsav II, Gobi Desert, Mongolian People's Republic.
Derivation of the name: Lat. *pulcher* — beautiful, because of a beautiful state of preservation.

Table 3

Dimensions of mandibles of *Proplatynotia longirostrata, Parviderma inexacta, Gobiderma pulchra, Saniwides mongoliensis, Paravaranus angustifrons* and *Cherminotus longifrons* in mm

Species and ZPAL cat. nos.	*Proplatynotia longirostrata* MgR-I/68	*Parviderma inexacta* MgR-I/43	*Gobiderma pulchra*		*Saniwides mongoliensis* MgR-I/72	*Paravaranus angustifrons* MgR-I/67	*Cherminotus longifrons* MgR-III/67
			MgR-III/64	MgR-III/65			
Total length	ca. 39	—	47	—	e. 44	—	—
Length without retroarticular process	35	e. 23	42	—	e. 38	—	—
Length of lateral dental margin	—	—	22.1	—	—	—	—
Length of splenial	13.5	—	ca. 12	—	ca. 17.2	—	—
Length of anterior ramus of coronoid in projection	6	4	6	5	9	—	2.6
Apex of coronoid to articular condyle	9.5	ca. 9	16	—	ca. 19	—	8.8
Anteriormost limit of supraangular to articular condyle lateral side	ca. 16.5	12	ca. 21	—	ca. 21	e. 12.2	12.1
Depth of postcoronoid ramus							
Maximum	3.6	2.7	6.5	—	5	1.8	1.6
In projection	3.6	2.7	4.5	—	3.1	1.8	1.6
Maximum depth of postcoronoid ramus to lateral length of supraangular	0.22	0.22	0.31	—	0.26	0.15	0.13
Depth of tooth bearing border	1.9	1.2	2.8	1.9	3.6	—	—

Diagnosis. — Skull subpentagonal in outline, its larger part posterior. Frontal paired but sometimes fusing with individual age. Posterolateral extensions of parietal close an angle of about 130°. An angle between paroccipital processes is only slightly less than this. Position of lacrimal foramen changing from prefrontolacrimal suture to lacrimal surface. Number of tooth positions is 11 on maxilla, 4 on premaxilla, 10 on dentary. Osteodermal skull covering of small-plate type or variable (anterior to the orbit).

Material. — Three specimens ZPAL MgR-III/64, 65 and 66 coming from Khermeen Tsav II and one ZPAL MgR-I/54 from Khulsan, a locality of the same age, are considered to be conspecific in spite of size and some other differences. The holotype, ZPAL MgR-III/64, has an almost perfectly preserved skull and two mandibles, only the quadrates and the jugal arches being damaged.

ZPAL MgR-III/66 lacks a premaxilla, a brain case, a right maxilla, a right jugal and both supratemporal arches. Left jugal arch is damaged. Both mandibles are preserved but damaged. Some poorly preserved vertebrae and fragmentary pectoral girdle are preserved with this species.

ZPAL MgR-III/65 consists of a damaged skull roof lacking a rostral part and maxillae. It has a strongly weathered brain case and a fragmentary right mandible with only one tooth. Remaining skull bones are missing or are deformed and pressed together. A thick covering of skull osteoderms is preserved over the skull bones.

ZPAL MgR-I/54 is a fragment of skull consisting of an anterior part of the frontals, the prefrontals, the nasals, the left lacrimal and a fragment of the right one, a posterior part of the left maxilla with one tooth and two tooth bases. The specimen is exactly like the specimens ZPAL MgR-III/64 and 66 as regards the proportions and mutual relations of bones but is somewhat bigger, not, however, reaching the size of the largest specimen from Khermeen Tsav, ZPAL MgR-III/65. It should probably be best compared with the last named specimen but is has only a few corresponding parts preserved. It differs from the specimens of *Gobiderma pulchra* coming from Khermeen Tsav by its more integrated osteodermal skull covering and its fused frontals and therefore probably merits a separate specific name. Because of its fragmentary preservation it is here assigned to the species *Gobiderma pulchra*, the differences (the fused frontals included) being regarded as a manifestation of the intraspecific variability.

Discussion. — *Gobiderma pulchra*, the only species of the necrosaurian grade represented by more than one specimen, displays a great amount of intraspecific variability, and mainly in size. The size differences amount to about 90% of the skull length of the smallest individual and could result from the phenomenon of triploidy (SZYMAŃSKI 1969). Measurements: see Tables 2 and 3.

Description. — **The skull as a whole.** The skull is subpentagonal in outline with its largest part posterior and the jugal arches only slightly laterally expanded. There is a certain amount of recession of the external nares which do not, however, wedge in between the nasals and the maxillae. The posterolateral extensions of the parietals are short and close an angle of about 130°, whereas the angle between the paroccipital processes is only slightly less than this. There is no division of the parietal into a medial part and lateral ones, the mandibular adductors being quite ventral of this bone. The parasagittal parts of both the parietals and the frontals as well as the anteromedial surfaces of the prefrontals are sculptured by rounded osteodermal thickening with perforated surfaces. Osteoderms of the same size and character cover the supratemporal fenestra, the orbit and the cheek region.

Skull roof. The premaxilla of *Gobiderma* is not unlike that of *Heloderma*. It differs from that of *Heloderma* by its palate processes extending somewhat more posteromedially and closing a more acute angle between them to which the premaxillary processes of the vomers are fitted. Two semilunar incisive processes enter this angle from anteroventral to underlie the premaxillary processes of the vomers. The curvature of the nasal process of the premaxilla indicates a depressed snout. The nasal process is long and narrow and overlaps the nasals by its posterior end, about

1/3 of its length, and is superficially wedged in between the nasal surfaces. The lateral margin of the premaxillary body is dorsally overlapped by premaxillary process and the anterior part of the medial process of the maxilla. There is probably no premaxillary foramen.

The nasals are subtriangular bones. The anterior borders are strongly anteriorly concave. The lateral side is sutured to the maxilla, prefrontal and frontal, the posterior angle of the nasal being bordered by the anterior processes of the frontal, which separate it superficially from the prefrontal as well as from the nasal of the other side. The bone surface is thickened by a bone tissue having been obviously deposited in continuity with the bone tissue of the nasals. The thickenings have not any determined pattern. They are separated by grooves and give a rather lumpy surface to the nasals. While getting thicker they change into rounded osteodermal units having a pitted surface and being still in continuity with the underlying bone. Their disposition is quite random. The osteodermal thickenings of the specimen ZPAL MgR-III/66, supposed to be a younger individual, bear a network of furrows, obviously of a vascular nature, instead of pits and recall the sculpture of young anguids (fig. 27B, C, F) as well as rudimentary sculpture of teiids (fig. 27E). The specimen ZPAL MgR-I/54 displays a much more integrated pattern of the osteodermal skull covering of the nasals and the prefrontals. By this specimen the osteodermal bone thickenings, of the same type as those of the Khermeen Tsav specimens, are united by a tuberous and pitted bone tissue into a continuous layer.

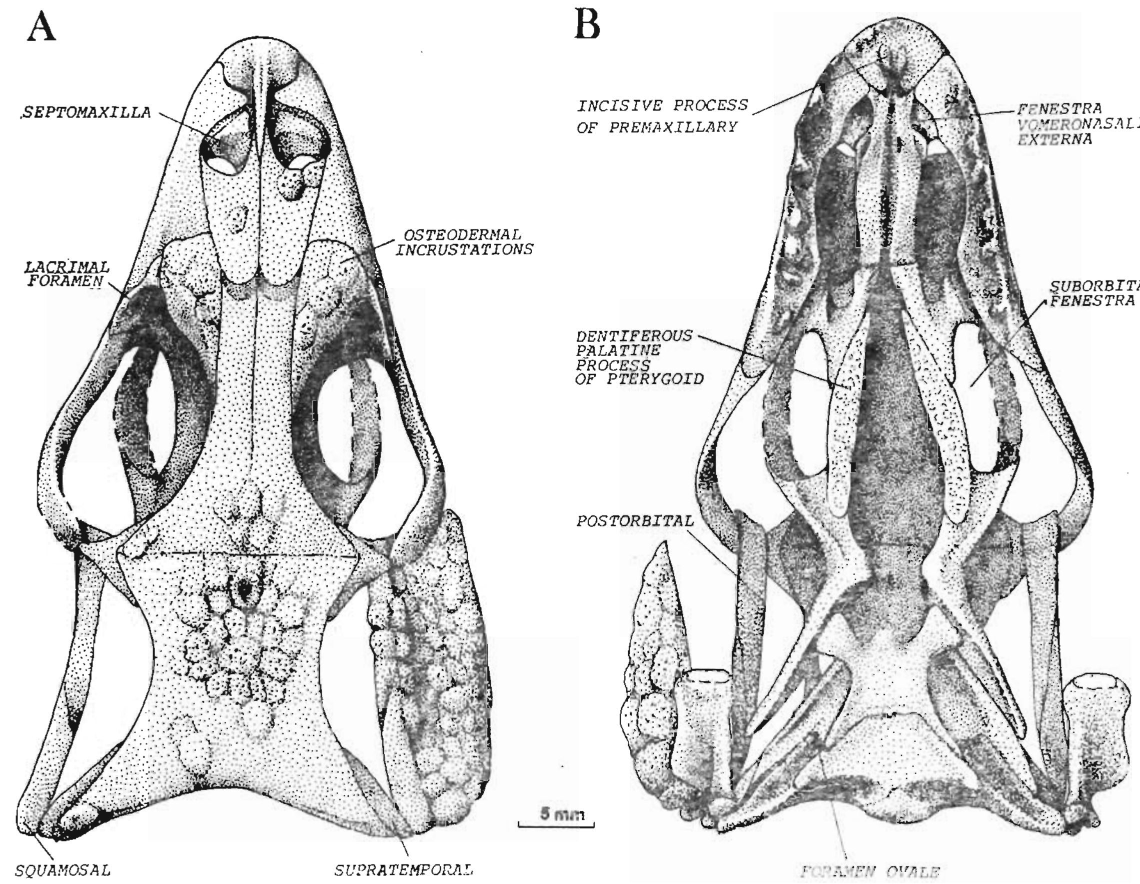


Fig. 11
Gobiderma pulchra gen. n., sp. n. Skull. A — Dorsal view, B — Ventral view.

The frontals are usually paired, but fused in ZPAL MgR-I/54, with straight parallel lateral margins diverging only posteriorly. They are completely separated from the maxilla by a long nasoprefrontal contact. The frontoparietal suture is straight and loose. The minimum width of the frontals is slightly less than 1/2 of their posterior broadening. The subolfactory processes extend separated from one another ventrally. They attenuate posteriorly and disappear in the broadened part of the frontals, about 1/4 of their length from the rear. The anterior part of the frontal surface situated between the prefrontals has numerous longitudinal thickening and furrows. Posterior to the prefrontal the lateral borders of the frontals are very much thickened and segmented. The segments, the size of the largest osteoderms of the same specimen but polygonal in shape, bear a dense net of furrows subdividing their surface into small irregular tubercles. About the midlength of the frontals these bordering osteoderms almost meet in the sagittal axis while diverging posteriorly (see fig. 27I). The triangular area they leave between them is subject to osteodermal small-plate incrustations exactly the same type as on the nasals. As judged from a comparison of the specimens ZPAL MgR-III/64 and 66 the furrowed surface of the young individual turns into a pitted surface in the older ones. The reason for that is obviously that the vascular furrows are externally covered by bone matrix in the ontogenesis leaving just openings for their exit to the skin.

The parietal recalls very much that of *Xenosaurus grandis.* Its length over the sagittal axis is almost the same (80%) as the lateral length. The dorsal surface of both the parietal main body and its posterolateral extensions is flat. The mandibular adductors are completely ventral to the bone. The width of the parietal at the frontoparietal suture is about the same as its sagittal length whereas its width at the posterolateral extensions is about 136% of the frontoparietal width. The maximum constriction is situated anterior to the midlength of the parietal and the parietal foramen is still more anterior. The sculpture of the parietal surface, which is the same type as that of the preceding bones, has a regular pattern. The parietal foramen has thickened borders. About the midlength of the parietal is a rounded osteodermal thickening surrounded by a circle of similar thickenings (see fig. 11A). Their surfaces are furrowed in the youngest specimen, furrowed or pitted in the next one and pitted in the largest one. By the anterolateral corners and on the whole posterior part of the bones, the bone thickenings are much weaker but sometimes overlain by loose osteodermal units produced within the skin clear of the skull bones and deposited on them only later on.

The maxilla is triangular in lateral view but has a nasal process extending from the anterodorsal side of the triangle onto the dorsal surface of the skull roof to meet the nasal and prefrontal. Anterior to the nasal process the anterior border of the maxilla slopes abruptly down bordering a much extended external naris. Its medial process reaches to the vomer. It overlaps both the premaxilla and the vomer from dorsal and sutures to the septomaxilla. The surface of the maxilla is almost bare of sculpture, only its nasal process having a somewhat lumpy surface. The posterior angle of the maxilla and its tooth bearing margin reach under the anterior part of the orbit. Here the maxilla is dorsally overlapped by the lacrimal and the jugal. The palatal shelf of the maxilla is very narrow, particularly so about the middle of its length. The palatomaxillary joint is very loose and almost parallel to the jaw axis. The septomaxilla is a triangular bone, dorsally concave, sloping both anteriad and posteriad.

The prefrontal extends to about half the length of the frontal and does not reach the frontal process of the postfrontal. It is tightly sutured to the frontal border. A subtriangular dorsal surface of the prefrontal has a protrudent and thickened orbital border. Medial to this border are three rounded osteodermal thickenings. The orbital lamina of the prefrontal extends in a vertical and transversal plane to meet the palatine. Laterally it is sutured to the lacrimal. In the holotype as well as in the specimen ZPAL MgR-III/66 it does not contribute to the bordering of the lacrimal foramen, which is completely shifted onto the lacrimal bone. However, the prefrontolacrimal suture is presumed not to be tightly fused and may give rise to the formation of a second lacrimal foramen characteristic of *Varanus* and *Lanthanotus*. In other specimens of *Gobiderma pulchra* ZPAL MgR-III/65 and ZPAL MgR-I/54 the lacrimal foramen is situated with in the prefrontolacrimal contact but the lacrimal tends to surround it from ventromedial in the second of these specimens. It follows that the lacrimal bone is subject to a large variability in *Gobiderma pulchra*, some of its states being morphologically initial to the states occurring in the modern platynotan families. The orbital border of the lacrimal is overlain by some osteodermal tubers whereas the lateral surface of the bone is concave (see pl. 7 : 1b).

The jugal is a laterally flattened bone wedged in between the maxilla and the lacrimal and making up a sliding joint with the postorbital judging by the surface of the latter (pl. 13 : 3b). The postfrontal is subtriangular. Its slender but not very long medial processes are tightly sutured to the frontal and the parietals, the sutures being much looser in the specimen ZPAL MgR-III/66. The postorbital contacts the postfrontal directly from the ventral side extending anterior to it, to contribute to the wall of the orbit (see fig. 11), but not lateral to it. Its lateral surface extends ventrodorsally to receive the end of the jugal. The shaft of the postorbital is fairly broad and long reaching almost the level of the anterior point of the supratemporal. The squamosal is a rather massive bone almost straight in dorsal aspect but curved ventrally at its posterior border to enter the dorsal incision of the quadrate. Its posterior part, more than a half of its length, is medially sutured to a long and broad dorsally flattened supratemporal. The anterior part of the squamosal is medially beveled for the contact with the laterally beveled part of the postorbital. The posterior part of the supratemporal turns ventrad parallel to the squamosal. It contributes to the quadrate joint.

Palatal complex. The vomers are long bones ventrally convex in transverse section. Similar to those of *Proplatynotia*, blunt crests extend from the maxillary processes over the whole length of the vomers. Medial to these crests the parasagittal parts of the vomers are concave in ventral aspect exactly as they are in *Proplatynotia*. Within this concavity a vomerine foramen for a medial palatine ramus of the facial nerve is clearly visible on each vomer. The length to width proportions of the vomer do not differ from those of *Proplatynotia* and *Saniwides* but the vomer seems narrower than that of *Proplatynotia* when compared to the important breadth of the fenestra exochoanalis. The anterior border of the vomer is produced laterally, both anterior and posterior to the fenestra vomeronasalis. The type of palate can be called palaeochoanate since the vomer and the maxilla are separated posterior to the fenestra vomeronasalis. This fenestra is posteriorly delimited by the septomaxilla. Posterior to it the lateral margin of the vomer bears a lacrimal furrow. The sagittal suture between the right vomer and the left one seems to be rather loose and the bones are split in their posterior half. Although the fenestra exochoanalis reaches far posterior as it usually does in Platynota, it is somewhat primitive in appearance because the vomerine and the maxillary processes are short and united by a concave bone lamina instead of being deeply separated. The maxillary process has a long and even furrow for articulation with the maxilla. The toothed pterygoid process of the palatine tapers posteriorly and is medially joined to the pterygoid, the joint being quite oblique. Instead of a shallow and narrow bone shelf it has an oblique medial wall for this articulation. Typical of the primitive Platynota the palatine process of the pterygoid is triangular, provided with a medial, convex toothed area separated by a concavity from the lateral margin. At the level of the basipterygoid joint there is a strong bend of the bone axis first medial, then lateral. Ventral from the joint the medial border of the pterygoid has a projection that prevents from its disarticulation. The structure of the pterygoectopterygoid joint is not quite clear. The ectopterygoid is a semilunar bone bordering the suborbital fenestra from lateral. It contacts the palatine and probably the maxilla with its anterior end but seems not to be laterally sutured to the jugal. The epipterygoids are preserved in the holotype only. They are slender bones round in transverse section. The quadrate has a very strong tympanic crest dorsally separated from the cephalic condyle by a broad incision. The medial crest is developed only just over the ventral extremity. The shaft of the quadrate is rather long. Its exact resting position is not known.

Occipital segment. The flat ventral surface of the brain case bears a distinct sphenoccipital suture of a trapezoidal type. The posterolateral extensions of the parasphenoid extend down to the anterior wall of the sphenoccipital tubercles. Their tops and much of their lateral walls are occupied by the epiphyses. The sphenoccipital tubercles project more laterally than ventrally. Sharp ventrolateral crests project laterally too, thus causing a broadening of the ventral surface of the sphenoid part. The basipterygoid processes have short and stout stalks ventrally convex in transverse section and strongly enlarged distally. Their articular surfaces are flat and semilunar in shape with straight dorsal margins. They project laterally, very much anteriorly and only a little ventrally. The sphenoccipital tubercles are situated about half a length of the occipital but are somewhat shifted posteriorly. The sphenoccipital toruses make up a posterior limit of the ventral surface of the brain case. Posterior to the sphenoccipital torus a concave surface for the rectus capitis anterior faces directly posteriorly (see fig. 21C; pl. 9 : 2). Originating from the tuberal crest just above the epiphysis the lateral ridge (fig. 20D) extends medially along the suture between the basioccipital and the exooccipital. This suture usually cuts the surface of the rectus capitis anterior. Here it constitutes a dorsal margin of this surface. Dorsal to the lateral ridge a slit-like semilunar foramen (or foramina) is an exit of the vagus nerve whereas medial to it is a hypoglossal foramen. The brain case is very flat and, thus, the crest running from the superior border of the foramen magnum is a sharp boundary between the posterior and the dorsal surface of the brain case. The area destined for the rectus capitis posterior faces directly dorsal, which must have some bearing on the function of this muscle. The occipital condyle is triangular in posteroventral view and foramen magnum is rounded but larger than high. The paroccipital processes make angles of slightly less than 90′ with the sharp tuberal crests. Their distal parts are extended in vertical plane. They have no ventral surfaces, their anterolateral surfaces facing antero-lateral but changing to a horizontal plane anteriorly. The posterior process of the prootic is directed to a dorsal corner of the paroccipital process but is also lateral to it and extended in a horizontal plane (see pl. 7 : 1a, figs. 20D, 22). The recessus vena jugularis is very broad and more exposed in ventral view than is the case in *Saniwides*. The sharp prootic crest slightly overhangs the jugular recess. It extends (see fig. 4D) from the basipterygoid process up to the end of the posterior process of the prootic running directly under the horizontal semicircular canal. The alar process extends much anterior from the anterior semicircular canal. It is separated from the inferior process by a deep trigeminal notch.

Mandible. The mandible is characterized by a strong sigmoid curvature recalling *Heloderma* (comp. figs. 9C and D). It occurs mainly in a vertical plane, the lower margin of the mandible being convex in its dental part and concave in the postdental one with a retroarticular process included. The postdental part is also medially concave as it is in *Heloderma* but the dentary is much straighter and narrower than it is in this genus. As differing from *Heloderma* the post-coronoid ramus of *Gobiderma* is very high. In a life position, the dentary is almost vertical whereas the postdental part increasingly inclines its lateral surface ventrolaterally. The curvature of the lower border is, thus, reduced because the ventrally projecting parts are directed medially. The development of intramandibular mobility is suggested.

The dentary is relatively longer, lower and more slender than it is in *Heloderma*. The Meckelian groove tapers anteriorly and turns ventrally. The plane of the symphysis is deflected ventrally from the plane of the dentary. The tooth-bearing border is boat-shaped and has no subdental ridge. The posterolateral margin of the dentary is covered by osteoderms and cannot be directly studied. But it is presumed to be nearly vertical and slightly concave (pl. 7 : 1a, fig. 9C). Its posterodorsal corner wedges in between the lateral and medial parts of the coronoid but it is not firmly sutured to this bone.

The splenial reaches anterior to about half the length of the dentary. Posteriorly it extends along less than half of the anterior ramus of the coronoid and is horizontally sutured to it. The splenial is rather loosely connected with the dentary. The anterior inferior alveolar foramen occurs at their contact. Posteroventral to it is an anterior mylohyoid foramen. The posterior margin of the splenial has an incision at the suture with the prearticular. Posteroventrally this margin is sutured to the angular. The coronoid has an anterior ramus extending horizontally and bifurcating at its anterior extremity and a posterior one descending posteroventrally from the apex almost to reach the ventral border of the mandible at its medial surface. The apex is situated in the middle of the bone and is strongly inclined medially from the surface of the mandible. The rami are separated by a deep and widely open notch. The ventral extension of the anterior ramus of the coronoid is probably about the level of the superior margin of the prearticular as judged from a horizontal bend of the splenial overlapping the coronoid. The posterior extension of the angular is at the level of the posterior end of the coronoid at the medial surface of the mandible while being more posterior at its lateral surface. The lateral surface of the angular tends to be covered by osteoderms with progressing age. The posterior mylohyoid foramen is presumed to be just anterior to the posterior margin of the splenial, the posterior mylohyoid nerve emerging by a slit between the splenial and the angular. The prearticular is sutured to the supraangular by a distinct suture extending horizontally to about half the length of the posterior ramus of the coronoid, then curving ventrally to border a small, oval mandibular fossa from front and from below. It surrounds the articular condyle from below and posterior, turning to the lateral surface of the mandible, then extends horizontally at the level of the upper wall of the retroarticular process to disappear under the angular. The dorsal margin of the supraangular is about the level of the dorsal margin of the anterior ramus of the coronoid. The osteodermal covering is still higher at the lateral surface of the mandible. The supraangular is produced medially to contribute to the formation of the glenoid.

Dentition. The lower teeth are bigger than the upper ones but both are the same type. They are subpleurodont, largely spaced with successive teeth preserved in the interdental position. The crowns are bilaterally flattened and have vertically folded bases, the folds being probably rather superficial. The number of tooth positions is about 11 in the maxilla, about 4 in the premaxilla and about 10 in the dentary.

MODERN PLATYNOTAN GRADE

Definition. — Platynotan lizards tending to development of a transverse pterygopalatine joint the type of hypokinetic axis instead of an oblique one and consequently to narrowing and shortening of anterior parts of palatine processes of pterygoid. External nares retracted to separate partially or completely maxillae from nasals. Nasals tending to fusion and atrophy, changing from paired plates through small unpaired bone to a rudiment or none. Tendency to development of an intramandibular jaw hinge with eventual formation of such a joint. Dentine folding tending to complication. Strong development of subolfactory processes, except cases of specialization. Postorbital and supratemporal regions specialized in different directions. Occipital region tending to specialization. Tendency to size increase. Tendency to reduction of osteodermal skull covering.

Discussion. — Modern platynotan grade is represented by four families: Varanidae, Lanthanotidae, Helodermatidae and Mosasauridae. The discrimination of the family Lanthanotidae, distinct from the Helodermatidae and the Varanidae, first substantiated by GADOW (1901), then by MCDOWELL and BOGERT (1954) and accepted by RIEPPEL (1980) is also admitted here. However, this taxonomic decision does not reflect the diverse possibilities of phylogenetic relationships between these families. Expressed by the former authors the opinion that the Lanthanotidae are more closely related to the Varanidae than to the Helodermatidae has been corroborated by RIEPPEL (1980) who indicated four derived character states of the head musculature shared by *Lanthanotus* and *Varanus* and not by *Heloderma*. It also agrees with my opinion advanced in the present paper (p. 61), based on the fossil evidence, that the similarities of the adaptive type of maxillary segment of skull existing between the Lanthanotidae and the Helodermatidae are due to convergence rather than homology. The geographic isolation of the helodermatids from the varanids and lanthanotids, although not quite conclusive, is also consistent with this view.

All the authors dealing with the problem of interrelationships of the platynotans suggest the monophyletic pattern of phylogeny of, what is called here, modern platynotan group, although the evidence presented does not exclude a polyphyletic pattern. The above quoted view concerning the relationships of the Helodermatidae would simply imply that this family has been isolated from the common stem earlier than other platynotan families (fig. 12, 13). The existence of a differentiated and widely spread group of necrosaurian lizards, shown in the present paper, suggests that the possibility of independent origin of the modern platynotan lizards from different necrosaurian groups should not be neglected. Among different versions of both patterns only these may be taken into account which accept the isolated position of the Helodermatidae among the modern platynotan groups (fig. 13).

The monophyletic origin of the modern platynotans (fig. 12A) is suggested by the uniformity of this group which is manifested by at least seven character states. These are as follows: a high degree of intramandibular mobility, a strong development of the subolfactory processes, a complicated dentine folding, a development of the transverse pterygopalatine suture of hypokinetic type, a retraction of the external nares, a tendency to size increase and to a reduction of the osteodermal skull covering. However, only one of them, the retraction of the external nares, may be regarded as a specialized feature shared by all the families, but it is not quite clear whether it is synapomorphy or not. The remaining character states are distributed in such a way that each of them is not shared by at least one platynotan family though not the same every time (see Table 5). Such a mosaic pattern of character state distribution within the modern platynotan group suggests the parallel development of its subunits.

A hypothesis of the monophyletic origin of the modern platynotans (fig. 12A) requires an ancestral species to be a generalized necrosaurian lizard having none of the specializations known at the modern platynotan grade but retracted nares (see Table 5). The improvement of the efficiency of the skull kinetic apparatus would be a new derived state achieved by this ancestor. This improvement is understood as an abrupt increase of intensity of the overretraction which is still dependent only upon an actual bending of the bony tissue of the pterygoid and is, thus, referred to as functional hypokinesis. It did not involve the formation of the structural hypokinetic axis at this early stage but stimulated its development at the later evolutionary stages, independent in different modern platynotan stems.

According to the second hypothesis (fig. 12B), the development of the modern platynotan group is a process of improvement of the predatory adaptations having originated at the necrosaurian grade or still earlier. In particular the type of palate, connected with overretraction, has gradually changed from a less derived (with an oblique pterygopalatine suture) to a more derived one (with a hypokinetic axis) owing to the common functional foundation of lizard skull kinesis and a similar adaptive goal. Correlated with this, other characters have gradually developed derived states independent in different lines. According to this hypothesis the modern platynotan families represent, in fact, only parts of monophyletic clades consisting of more primitive (necrosaurian) and more derived (modern platynotan) subunits.

The state of functional hypokinesis, which is suggested by the first hypothesis to be a shared and derived feature of the modern platynotans, is, in fact, difficult to be isolated as a separate

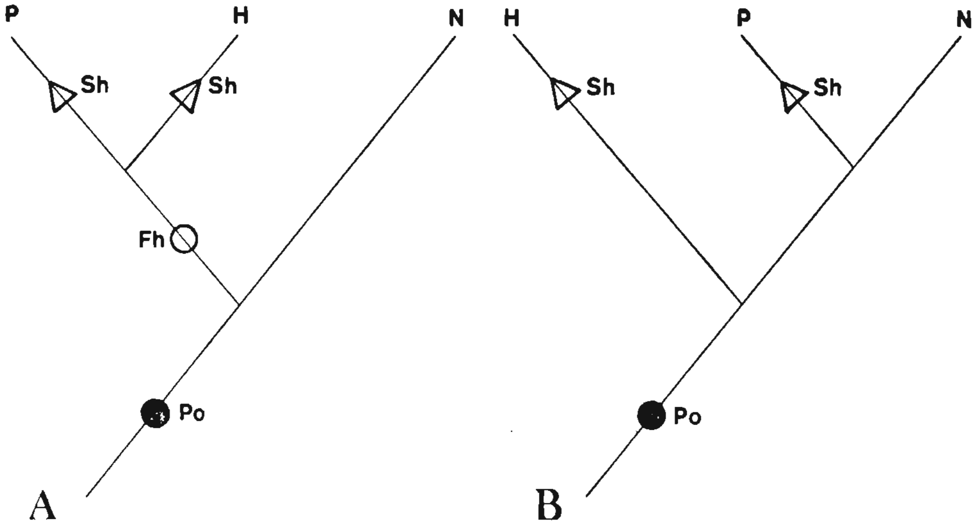


Fig. 12
Cladogram illustrating possible methods of affiliation of the modern platynotan groups upon the necrosaurian stem (N) (see also fig. 13). Relationship between the helodermatids (H) and the remaining modern platynotans (P). A — Monophyletic pattern; abrupt change of the primitive type of the overretraction (Po) into the functional hypokinesis (Fh). B — Polyphyletic pattern; gradual transition of the primitive type of the overretraction into the structural hypokinesis (Sh). Solid black circles — primitive character states; open circles — derived character states; triangles — parallelisms.

event from the continuous development of the skull kinesis and the same is true of the retraction of the external nares. Therefore the second hypothesis is favoured here but its details may still be subject to discussion.

Helodermatidae first appear in the Oligocene of North America (Gilmore 1928) but the Late Cretaceous species *Paraderma bogerti*, known from the Lance Formation (Late Maastrichtian, Clemens 1960) is very similar (Estes 1964) to *Heloderma* and may belong to this family. Being unknown from Asia this family probably derived from the American necrosaurid lizards and did not leave the American continent until the Late Eocene (Hoffstetter 1962). In contrast, the Lanthanotidae and the Varanidae have been Asiatic families since the Late Cretaceous and are, possibly, to be derived from Asiatic necrosaurians.

From two alternative hypotheses (fig. 13) illustrating the different concepts of relationships between the Varanidae and the Lanthanotidae I would prefer the first one (fig. 13A). Although four derived character states of the musculature shared by *Lanthanotus* and *Varanus* point to their being sister groups, the distribution of states of these characters cannot be studied in fossil forms. They are, thus, not conclusive as regards the interrelationships of Asiatic Platynota and the relationships of the Mosasauridae. A whole array of derived osteological features, which are in common in *Lanthanotus* and *Varanus* and seem, thus, to support their close ralationship, are parallel achievements in my opinion. Among them I would number the restriction of metakinetic movement through the broad contact between the supraoccipital and the parietal. It is clearly correlated with the overall type of skull kinesis manifested by proportions of parietal and snout units and those of the brain case which are quite different in both families and should have developed independently. It cannot thus, be regarded as synapomorphy, as Rieppel (1980) suggests but is parallel at the best. I would also question the synapomorphic nature of fused nasals which clearly result from the increase of the external nares characteristic of all the modern platynotans. This is supported by the doubled nature of this bone in primitive representatives of both families, *Cherminotus* and *Saniwides*. These genera are also indicative of parallel development of some other specializations shared by the families

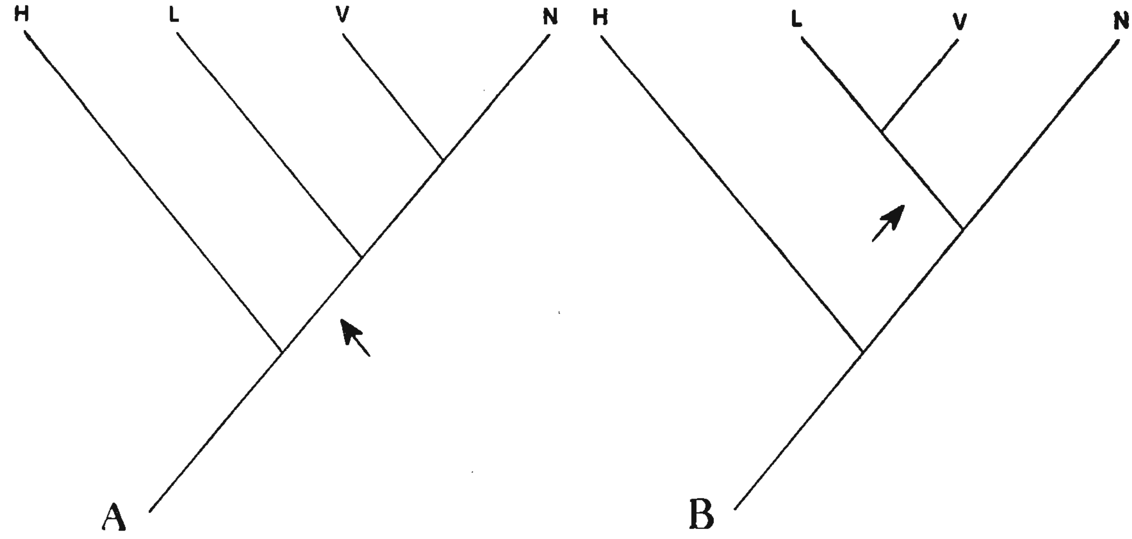


Fig. 13
Cladograms illustrating possible methods of affiliation of the modern platynotan groups upon the necrosaurian stem (continuation of fig. 12). Relationship of the Helodermatidae as in fig. 12B. A — Polyphyletic origin of the Lanthanotidae and the Varanidae; B — Monophyletic origin of these groups. The arrow denotes a position of the common ancestor.

in question, such as a doubled, although differing in details, lacrimal foramen (single in *Saniwides*) and a long anterior extension of the rectus capitis anterior manifested by a derived shortened type of sphenoccipital suture (less derived, trapezoidal type in both *Cherminotus* and *Saniwides*). I would agree with the final conclusion of RIEPPEL (1980) that the common ancestry of the Lanthanotidae and the Varanidae must be very remote. The lanthanotids, which are represented by small lizards even in the Late Cretaceous (see p. 61) are not likely to have been secondarily derived from any large sized animals. Their ancestors should be looked for within small-sized or variable-sized necrosaurian groups (fig. 13A). I would suggest that they represent a line of small predators from the very beginning of their phylogeny, most fo their derived features having been developed as an adaptive entity along with small size.

The Mosasauridae are typical modern platynotan family displaying, among others, the retracted external nares, the intramandibular joint and the functionally hypokinetic palate (RUSSELL 1967). According to the above accepted hypothesis these character states result from the development of the common structural and adaptive foundations occurring at the early stage of phylogeny of the Platynota. A great number of uniquely derived character states, such as fused frontals of triangular outline, atrophied nasals, a peculiar premaxillofrontal contact and a unique structure of the quadrate as well as their early appearance in fossil state are indicative of both the early divergence of the Platynotans and a very rapid rate of evolution in this family. As far as is known, the structure of the early relatives of the family, the Aigialosauridae (KORNHUBER 1901, KRUMBERGER 1892, RUSSEL 1967) corresponds to the necrosaurian grade of the platynotan evolution, which also corresponds with the above statements. MCDOWELL and BOGERT (1954) pointed out the similarities existing between the Aigialosauridae and the Lanthanotidae in the structure of the mandible, and precisely of the intramandibular joint, and that of limbs, which, in their opinion, support the aigialosaurian affinity of *Lanthanotus*. However, the similarities in the structure of the intramandibular joint are merely those of grade and only indicate that the groups in question are equally well advanced in the process typical of all platynotans. Advocated by RIEPPEL (1980), the relationships between the Varanidae and the „aigialosaurian group" (*sensu* MCDOWELL and BOGERT 1954) based on the shared proportions of the skull as a whole, of snout and skull table as well as on the complete upper temporal arch seem more reasonable. However, these character states are shared by all lizards of the necrosaurian grade too and, thus, ought to be regarded as primitive in the platynotans.

I would conclude that the superfamily Platynota was represented by diversified and widespread lizards having attained the necrosaurian morphological grade about the late Jurassic (*Proaigialosaurus* KUHN 1958) and early Cretaceous time. Most of them survived until the late Cretaceous. The Necrosauridae, Aigialosauridae, Dolichosauridae and some genera not assigned to families would represent this grade. Modern platynotan families have evolved from different necrosaurians, the Aigialosauridae being probably directly ancestral to the Mosasauridae according to Russel (1967). Necrosaurian ancestors of the Varanidae and the Lanthanotidae may not be indicated for the time being, neither may the possible interrelationships between the necrosaurian groups be reconstructed.

The Late Cretaceous representatives of the Varanidae, the genera *Saniwides* and *Telmasaurus* from Mongolia, are perfectly fit to fill the gap between the necrosaurian and the modern platynotan grade with their oblique pterygopalatine joint, toothed palatines and pterygoids as well as with their probably less retracted external nares. The Late Cretaceous representative of the Lanthanotidae, *Cherminotus*, is more typical of the modern platynotans.

Family **Varanidae** HARDWICKE and GRAY, 1824

Supplementary diagnosis. — Platynotan lizards with parietal strongly constricted by surfaces for mandibular adductors. Supratemporal fossae large. Supratemporal arcade present. Postfrontal fused with postorbital into a roughly x-shaped bone, their sutures occasionally preserved. Tendency to shortening of parietals and to lengthening of snout. Brain case shorter and higher than usual in the Platynota, with alar processes directed anterodorsally. Teeth usually sharp, subpleurodont to pleurodont with dentine folding tending to complication. Intramandibular joint not advanced beyond necrosaurian level: long, horizontal coronoid-splenial contact. Skull long, subtriangular, of medium to large size. No osteodermal covering fused to skull surface.

Genus *Saniwides* nov.

Type species: *Saniwides mongoliensis* sp. n.

Derivation of the name: The name *Saniwides* indicates the similarity to the North American, Eocene genus *Saniwa* LEIDY, 1970.

Diagnosis. — Medium-sized varanid lizards. Frontals paired. External nares retracted but not to interrupt the nasomaxillary contact. Rostral part of skull very flat. Vomers medially separated. Jugal not separated from postorbital but movably articulated with it. Squamosal long and slender, laterally concave and reaching far anteriorly almost to touch the jugal. Parietal foramen anterior to the midpoint of the presumed parietal length. Pterygopalatine suture oblique, but anterior process of pterygoid very weak. Palatines and pterygoids toothed. Variable number of lacrimal foramina. Subolfactory processes strongly developed, not fused ventrally. Sphenoccipital tubercles situated about half the length of basioccipital instead of being shifted to its foremost part. Tuberal crest short subvertical instead of being a long subhorizontal and laterally enlarged crest usually observed in *Varanus*.

Stratigraphical and geographical range. — Genus monotypic; known from the type horizon and locality.

Discussion. — The genus *Saniwides* is assigned to the family Varanidae on the basis of the overall platynotan character of its skull, mandible and teeth associated with the varanid structure of the parietal and supratemporal region. Its being one of the primitive representatives of the family can be proved by the following character states: the state of external nares is less derived, i. e. less retracted than is the case in *Varanus*. Both pterygoids and palatines are toothed. The sphenoccipital tubercles are situated about half the length of basioccipital instead of being shifted to its foremost part as they usually do in *Varanus*. Although this character is subject to a certain variability in the latter genus, the majority of its species (figured by MERTENS 1942) display a derived, anteriorly shifted position of these tubercles, only few [*V.* (*Odatria*) *acanthurus branchyurus* and *V.* (*Indovaranus*) *bengalensis nebulosus*] being primitive in this regard.

The similarities between *Saniwides* and the Eocene North American genus *Saniwa* LEIDY mainly consist in the common differences relative to *Varanus*. Some of them, such as the toothed palate and the position of the sphenoccipital tubercles, suggest a less advanced stage in the varanid line of evolution. Some others (such as a similar structure of the pterygoid, its ectopterygoid process being separated from the toothed surface by a concavity and bordered by ventral and dorsal crests from the lateral side, and the shape of the retroarticular process with the hook-like internal ventral expansion of its posterior end) are probably mere coincidences.

ESTES (pers. comm.) suggests that *Saniwa* may prove to be congeneric with *Varanus*, the differences between them, pointed out by GILMORE (1928), being of a specific rank only. Even if true, this supposed congenerity cannot be extended over *Saniwides* in spite of the above mentioned similarities between this genus and *Saniwa*. *Saniwides* is probably more primitive than *Saniwa* in having a long, although very narrow, anterior process of the pterygoid and consequently an oblique pterygopalatine joint instead of a presumed more transverse one in *Saniwa*. The toothed surface of the pterygoid is much broader in *Saniwides*. The postorbitofrontal is much more robust, its postorbital process much longer and wider and the squamosal reaches much further anteriorly than is the case in *Saniwa*. The differences in perforation of the lacrimal, are presumed to be a manifestation of an intrafamilial variability rather than to represent evolutionary levels. Another difference between the genera compared is the number of teeth which is exactly the reverse of what could be expected assuming the platynotan trend towards a reduction of the tooth row. The Eocene *Saniwa ensidens* is much more primitive with its 24 maxillary tooth positions (if the number given by GILMORE 1928 is correct) than the Upper Cretaceous *Saniwides mongoliensis*.

Saniwides mongoliensis sp. n.

(pls. 8, 9: 3, 4; figs. 9B, 14, 20E)

Holotype: A skull ZPAL MgR-I/72.
Type horizon: Upper Cretaceous, ?middle Campanian, Barun Goyot Formation.
Type locality: Khulsan, Nemegt Basin, Gobi Desert, Mongolian People's Republic.
Derivation of the name: *mongoliensis* — from Mongolia.

Diagnosis. — Skull triangular about 4.5 cm in length. Short, rounded orbits. Teeth rather thick and blunt. Number of tooth positions: about 16 in maxilla, about 4 in premaxilla, about 15 in dentary. Upper tooth row reaching beneath anterior part of orbit. Postcoronoid part of mandible curved to face dorsomedially instead of medially.

Material. — The holotype ZPAL MgR-I/72, the only specimen known, is a skull with a mandible, both incomplete and deformed. The skull lacks the posterior part of the parietals, their posterolateral extensions being reconstructed (fig. 14) from the position of distal extremities of paroccipital processes. As an artefact of preservation, the snout unit of the skull is strongly retracted, whereas the brain case strongly protracted. Owing to this unnatural position the right basipterygoid joint is disarticulated, whereas the left pterygoid is shifted forwards up to the vomer, thus causing a strong abduction of the lateral part of the snout unit, and the corresponding left basipterygoid process is broken off under the pressure of the pterygoid. The left ectopterygoid is turned to a position almost perpendicular to the jugal. The above deformations imply (1) a natural ability of the lateral parts of the snout unit to abduction, (2) a limitation of the union of the ectopterygoid with the jugal to a diarthrosis of its anterior end, the shaft changing a position relative to the jugal; (3) association of metakinetic mobility with the retractive function of the lizard skull apparatus, retraction of the pterygoid relative to the brain case being limited by the basipterygoid processes.

A very oblique position of the palatine producing a hollow shape of the palate, although stressed by deformation, is probably close to a natural disposition. The mandibles are missing their anterior tips. Their postcoronoid rami are broken and bent medially. The left mandible has its dentary bent lateral and disjointed from the splenial thus suggesting a lateral mobility of the jaw in the intramandibular joint.

The skull has been found in association with some damaged neck vertebrae.

Measurements. — See Tables 3 and 4.

Description. — Skull as a whole. A subtriangular skull of the varanid type with an elongated snout and a shortened parietal. As judged from the anterodorsal border of the maxilla, these bones are separated from the nasals by external nares. The parietals bear surfaces for the mandibular adductors facing laterally. Supratemporal fossae are large. There is no osteodermal skull covering.

Skull roof. The unpaired premaxilla has a horse-shoe shaped body, broader than long. Its processes are strongly damaged. Two semilunar incisive processes project ventrad of the palatine surface. Their contact with the vomer is unknown.

The outline of the nasals, which are missing from the specimen is reconstructed (fig. 13) basing on the surface of the overlap of the right one on the frontal as well as on a medial margin of the maxilla (see pl. 8 : 1a).

The frontals are paired with straight, lateral margins diverging only posteriorly, their anterior breadth being about 0.43 of the maximum one. They border the nasals medially and laterally by means of anteriorly projecting processes. The lateral process has probably a short contact with the maxilla. The subolfactory processes extend ventrally and medially but do not meet one another in the midline. They attenuate posteriorly and disappear about 1/4 of the frontal length from their rear. The frontals bear two pairs of osteodermal bone thickenings situated near their lateral borders. The frontoparietal suture is straight. The frontoprefrontal suture is straight too. It runs in a parasagittal plane and is very loose. A supposed entire length of the parietal is about 0.7 of the frontal length. The parietal is constricted about the middle of its supposed length by means of distinct external parietal crests. The parietal foramen is anterior to a half of the supposed parietal length.

The nasal process of the maxilla bends medially onto the dorsal surface of the skull. It is presumed to have a medial border (instead of an apex) which is parallel to a sagittal axis of the skull and produces a nasomaxillary suture. This border slopes anteriad beginning approximately half way back on the snout to delimit the external nares. The posterior side of the maxilla is overlapped by lacrimal medially and jugal laterally. The palatal shelf of the maxilla is limited to the tooth bearing border in the anterior part while extending a little medially to meet the maxillary process of the palatine. The maxilla reaches under the anterior part of the orbit.

The prefrontal is rather broad and short. Its posterolateral border is convex laterally and overhangs the orbital lamina. The supraorbital process is very short and does not protrude very much from the body of the bone.

The lacrimal is a plate of bone stretching more lateral than posterior. It is pierced by a lacrimal foramen, which is entirely within this bone, and is probably the only foramen in the lacrimal region. As judged from its preserved parts, the jugal has only a slight lateral bending. Its posterior end makes a sliding joint with a postorbitofrontal.

The postorbitofrontal is an x-shaped bone. Its posterolateral process, which is a part of

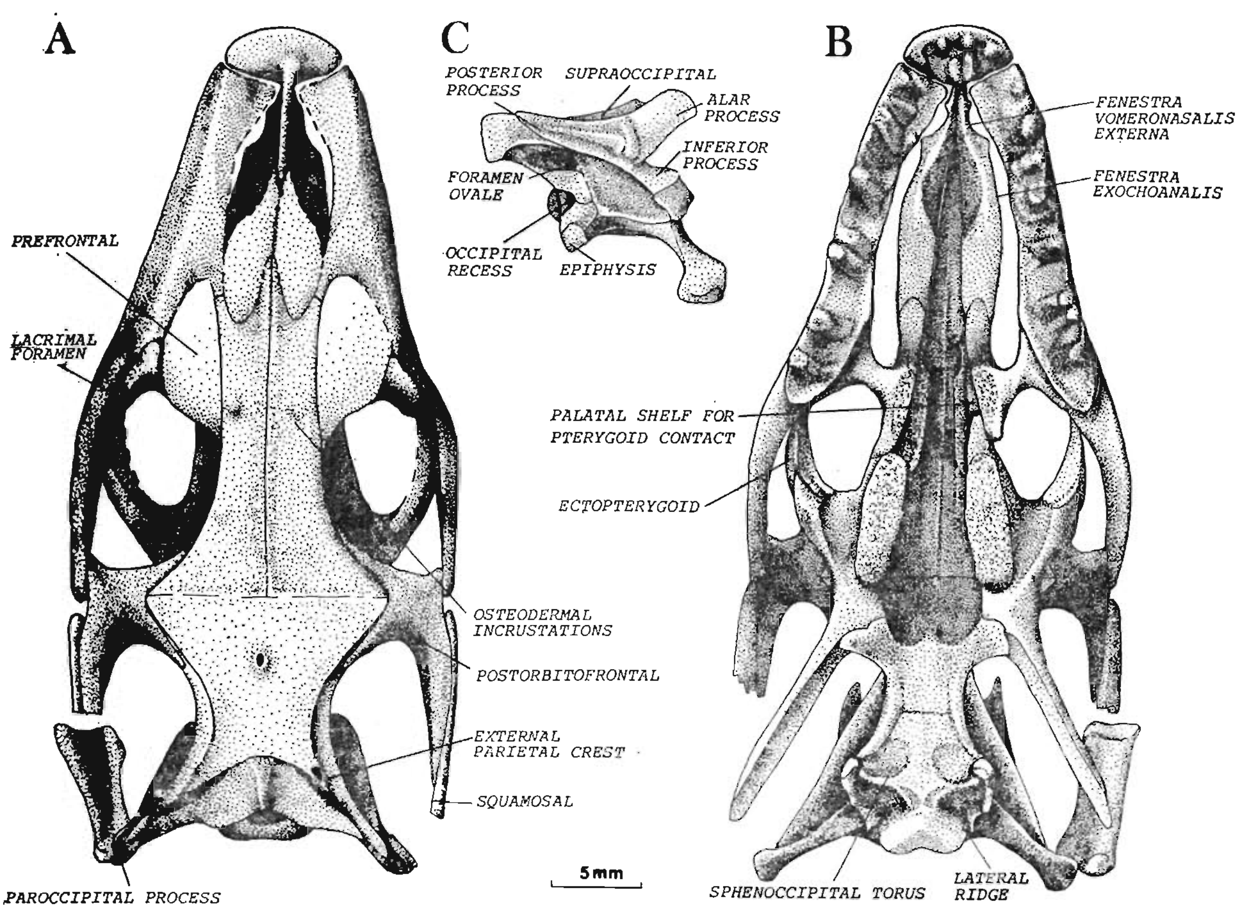


Fig. 14
Saniwides mongoliensis gen. n., sp. n. Skull. A — Dorsal view; B — Ventral view; C — Brain case in right side view.

a postorbital, is the longest and the strongest of its four processes. The medial processes are long and slender, the frontal one being broadly separated from the prefrontal. They closely fit the lateral borders of the frontal and parietal but the sutures are loose. The anterolateral process is short and produced ventrally. Its lateral wall receives the end of the jugal. The squamosal adjoins the posterolateral process of the postorbitofrontal reaching up to the jugal. The course of its anterior part is parallel to a sagittal axis, the posterior part is unknown.

Palatal complex. The vomers are rectangular and rather flat bones. They are narrow and long. Their anterior ends are produced into long premaxillary processes bordering fenestra vomeronasalis medially. The nature of contact between this fenestra and the fenestra exochoanalis is not clear. There is no sagittal suture between the vomers, a situation permitting an important amount of abduction. Posterior to the premaxillary processes the medial margins of the vomers are concave at about less than a half of their length. They contact the vomerine processes of the palatines which come from a posteroventral direction. These processes of the palatines do not reach anterior as far as the palatomaxillary suture does. The maxillary process of the palatine is very well separated from the vomerine one by a much retracted choana, the posterior wall of which is vertical. The palatomaxillary suture is rather loose and slightly oblique relative to a sagittal plane. The pterygoid process of the palatine is a rather broad and flattened band of bone situated in a horizontal plane, i. e. in a plane strongly bent relative to the more anterior parts of the palatine. The pterygoid process is subdivided into a broad platform bearing small numerous densely spaced teeth and a very narrow shelf situated deep to its surface and destined for the anterior process of the pterygoid.

The palatine process of the pterygoid is widely separated from the posterior end of the vomer. It has a long oval toothed surface passing into a long and narrow triangular anterior extension. Separated from it by a concavity is the ectopterygoid process of the pterygoid. The lateral border of this process is produced ventrally into a longitudinal crest to receive the pterygomandibularis. The anterior part of the ectopterygoid process articulates from medial and ventral with the ectopterygoid. The quadrate process is triangular in transverse section in its anterior part while getting laterally flattened posteriad. Its axis is strongly bent relative to the main axis of the palatine process.

The ectopterygoid is articulated with the jugal by its anterolateral end only. It borders the suborbital fenestra completely excluding both the maxilla and the jugal from its margins. The epipterygoids are lacking from the specimen. The quadrate has almost no tympanic crest and a rather narrow medial crest which is, however, more extended ventrally. The posterior crest is strongly protruding and curved posterodorsally.

Occipital segment (figs. 20, 21, 22, 14C, pl. 9 : 3). The sutures of the brain case are fused at the type specimen, but the sphenoccipital suture of the trapezoid type is quite distinct. The posterolateral extensions of the parasphenoid reach down to the tops of the sphenoccipital tubercles made of epiphyses. The sphenoccipital tubercles project more ventrally than laterally. Extending from the posterolateral corners of the basipterygoid processes down to the sphenoccipital tubercles are distinct ventrolateral crests. The basipterygoid processes have short and stout stalks ventrally convex in transverse section and strongly enlarged distally. They project anteroventrolaterally. The tops of the sphenoccipital tubercles are situated at the level of about half the length of the basioccipital. Running over the medial surfaces of the sphenoccipital tubercles from their tops towards a midpoint of the occipital condyle, the much protruding sphenoccipital toruses make up a posterior limit of the ventral surface of the brain case. Posterior to the sphenoccipital torus is a concave surface for the rectus capitis anterior. It is delimited by a strongly protruding tuberal crest laterally and by a lateral ridge dorsolaterally. The lateral ridge is a weak crest diverging from the tuberal crest and directed to the occipital condyle. Dorsal to it is an area destined for the longissimus cervicis (see pl. 9 : 3, comp. fig. 21). Within this surface there is a slit-like vagus foramen and, more medial to it, a hypoglossal foramen. Running horizontally from the dorsolateral margin of the foramen magnum and attenuating laterally, a crest separates the area of the longissimus cervicis from a triangular concave area destined for the rectus capitis posterior, which is superior to this crest and facing more posterior than it usually does. A completely fused prooticosupraoccipital suture, projecting as a sharp crest, is an upper rather than an anterolateral limit of this muscle area and a superior margin of the paroccipital process at the same time. The inferior margin of this process is lateral continuation of the tuberal crest with which it makes an angle of about 90°. Just at the junction of both, the inferior margin of the paroccipital process produces the crista interfenestralis extending towards the prootic. The distal extremity of the paroccipital process faces directly posterior and is dorsoventrally englarged. It probably received the obliquus capitis. Its anterolateral surface is situated vertically and the posterior process of the prootic is directed to its dorsal corner (fig. 14C). A recessus vena jugularis is spacious but extending vertically rather than horizontally, and is not largely exposed in ventral aspect. It is overhung by a sharp prootic crest extending from the posterior margin of the basipterygoid process up to the anterior semicircular canal and then along the horizontal semicircular canal towards the dorsal corner of the distal extremity of the paroccipital process. Only beyond the extent of the prootic does it abruptly turn to the ventral corner of this processs, yet does not seriously alter a general vertical disposition of this part of the brain case, which is, thus, quite modern in this regard. A trigeminal notch cuts deeply into the prootic, both the inferior process and the alar process extending far anteriad of the anterior semicircular canal as they do in platynotans. The prootic process is slightly bent dorsolaterally and the supraoccipital ascends anteriad, foreshadowing or even representing a high skull type of varanids. The character of the metakinetic joint is not known. The prooticosupraoccipital suture is probably not fused anteriorly to produce an incision of the brain case margin excatly as it does in Varanus.

Mandible (fig. 9E). Both rami of the mandible are subject to deformations and, thus, the exact shape of the bone must be reconstructed. However, almost all component bones are preserved except for the anterior parts of the dentaries. The mandible was certainly curved medially in its postcoronoid part as demonstrated by the right ramus, whereas the sigmoid curvature displayed by the left ramus is probably mostly an artefact of preservation. The right ramus has its ventral margin straight.

As judged from the preserved part of the posterolateral margin of the left dentary and the trace of this margin left on the right supraangular and angular, this margin was vertical, slightly concave and situated anterior to the coronoid level. The tooth-bearing surface is strongly beveled. There is no subdental ridge but the subdental margin of this surface is thick, much more like that of *Proplatynotia* than like *Gobiderma.*

The anterior extension of the splenial is to about half the estimated length of the dentary. Its anterior part turns from the medial surface of the mandible to its ventral border as does the Meckelian fossa. The posterior extension of the splenial is presumed to be further than half the length of the anterior ramus of the coronoid (considered from its apex to its contact with the dentary). This is based on the traces left by the splenial (fig. 29, sp surface) on the ventral part of the coronoid as well as on both, the prearticular and the angular.

As typical of Platynota the coronoid has a long horizontal anterior ramus connected but quite loosely with the dentary. Its posterior ramus is short and delicate. The coronoid is strongly medially deflected as a whole from the plane of the mandible to produce a posterior concave surface for the adductor mandibulae. Owing to the damage to the splenial and to the dentary the exact extent of their overlap on the angular cannot be stated. The posterior mylohyoid foramen was probably covered by the splenial (see pl. 8 : 3a) and so the posterior mylohynid nerve was forced to emerge through a slit between the angular and the splenial or the foramen was situated just posterior to the splenial margin. At about the level of the coronoid apex the angular turns completely onto the lateral surface of the mandible. Its posterior extension is probably larger than that of coronoid on this surface of the mandible. Connected with its medial curving, the postcoronoid part of the mandible is twisted so that its lateral surface, made of the angular, the prearticular and the supraangular, gradually turns ventrad. Apart from that, the mutual relations of the prearticular and the supraangular are quite usual. The retroarticular process is a quadrangular bone with its posteromedial corner strongly projecting posteromedially and a concave dorsal surface.

Dentition. The teeth are largely spaced with successive teeth preserved in some interdental spaces pointing to the interdental tooth replacement. They are firmly ankylosed to the jaws not only by their bases but also by almost their whole lateral surfaces, only small parts of their crowns protruding over the jaw margins and are, thus, more typically pleurodont than in any Anguimorpha which are said to be subpleurodont. The tooth bases are thrown into folds which are rather scarce and usually superficial but sometimes reach to the medullar cavity. Each tooth has a basal foramen. The teeth are columnar in shape but get narrower distally when unworn. Their sections are round. About 16 tooth positions with about 10 preserved teeth are present in the maxillary tooth row which extends under the anterior part of the orbit. About 13 tooth positions with 7 teeth are present on the preserved part of the dentary estimated as 80% of this bone.

Genus *Telmasaurus* GILMORE, 1943

Type species: *Telmasaurus grangeri* GILMORE, 1943.

Stratigraphical and geographical range. — Bayn Dzak, Khulsan, Gobi Desert, Mongolian People's Republic. ?upper Santonian and/or ?lower Campanian, Djadokhta Formation; ?middle Campanian, Barun Goyot Formation.

Telmasaurus grangeri GILMORE, 1943

(pls. 9 : 1; 10 : 1; figs. 4G, 15, 16, 20C, 21D)

Geographical and stratigraphical range. — As for the genus.

Material. — A specimen ZPAL MgR-I/65 from Khulsan is a skull lacking a preorbital part. The palate and the quadrates are damaged. Two damaged anterior cervical vertebrae are present with the skull.

Discussion. — The specimen ZPAL MgR-I/65 does not differ from the preserved parts of the holotype AMNH 6645 but by its slightly smaller size. The similarities refer to such specific character states as a far posterior situation of a least diameter of the parietal; its long posterolateral extensions and its dorsal quadrate articulation shifted far away from the parietal main body. The differences in the structure of the postorbitofrontal result from the state of preservation as well as from the presence of the postorbitopostfrontal suture on the ventral surface of this region in AMNH 6645. This feature is a subject to intraspecific variability even in recent *Varanus*. The presence of the parietal foramen in the specimen ZPAL MgR-I/65 is another difference relative to *Telmasaurus grangeri*. The holotype of this species, AMNH 6645 lacks this foramen, the opening described as a parietal foramen by GILMORE (1954: 380) being a pit for the parietal ligament, in fact. However, in view of the identity of all other preserved parts of the specimens compared, I would rather incline to assume an intraspecific variability of the parietal foramen, possibly tending to disappear in *Telmasaurus*, than to negate their conspecificity.

Measurements. — See Tables 3 and 4.

Description. — Skull roof. All the bones of the skull roof are bare of the osteodermal incrustation, the only sculpture displayed being the concavity of the external surface of these bones. The frontals are firmly fused in sagittal axis. Extending along the suture line on both the dorsal and the ventral surfaces of the bones is a protruding crest. The lateral border of the frontal projects dorsally thus making a dorsal surface of each frontal and that of both of them concave in transverse section. The region of maximum constriction of the frontals is situated at about half a length of them, while increasing slightly anteriad and strongly posteriad. Their anterior breadth is about 0.4 and the minimum breadth about 0.33 of the maximum one. The subolfactory processes are very well developed. They project both ventrally and medially but are separated by a small gap at their distal parts. They attenuate from about the middle of the frontal length and disappear about 1/4 of this length from the frontoparietal suture. The frontoparietal suture is slightly denticulate and convex anteriorly. It probably tended to fuse in ontogeny.

The length of the parietal main body is about 65% of the frontal length. Its breadth at the frontoparietal suture is 1.3 of its length but it is only 0.4 of this length at the maximum constriction of the bone, just anterior to the posterolateral extension. The posterolateral extensions of the parietal are as long as the main body. Delimited by external parietal crests and a nuchal crest, the dorsal surface of the parietal is concave. It continues a small distance along the posterolateral extension while tapering distally, then passes into its dorsal acute margin. Extending ventrolaterally of the external parietal crest, the lateral surface of the parietal is diversified into a low anterior part facing laterally and a posterior deeper part facing more dorsolaterally. The anterior part, corresponding to the parietal main body, has a contact with the anterior part of the alar process, the parietal process of the postfrontal and probably with the epipterygoid, whereas the posterior one, which is a lateral surface of the posterolateral extension of the parietal, receives the origin of the mandibular adductors. The angle between the posterolateral extensions of the parietal is about 60°. Medial surfaces of these extensions are diversified into a lower and an upper part. The lower part faces medially at the distal end of the process but turns ventrally in its proximal part. The upper part extends over half the length of each posterolateral extension and is the only medial surface in their proximal parts. It bears a horizontal furrow, a possible place of insertion of the spinalis capitis, in the parasagittal region as well as the origin of the depressor mandibulae, more lateral than that. Lying anterior to the midlength of the parietal main body is a small parietal foramen artificially enlarged on the left side (pl. 9 : 1a).

The maxilla is not preserved except for the posterior fragment of the narrow palatal shelf. It probably did not reach beneath the orbit. Only posterior part of the prefrontal is preserved. Its posterior process largely enters into the orbit overhanging its anteromedial part. It reaches almost the postfrontal not, however, touching it. Running parallel to a sagittal axis, a dorsally projecting crest borders the dorsal surface of the bone thus making it dorsally concave. It overhangs a horizontal furrow running as usual, across the anterior margin of the orbit. Directly below this furrow is a fragment of the lacrimal bearing a small foramen, probably a lacrimal foramen. Medial to it is a second slit-like lacrimal foramen situated at the prefrontolacrimal suture.

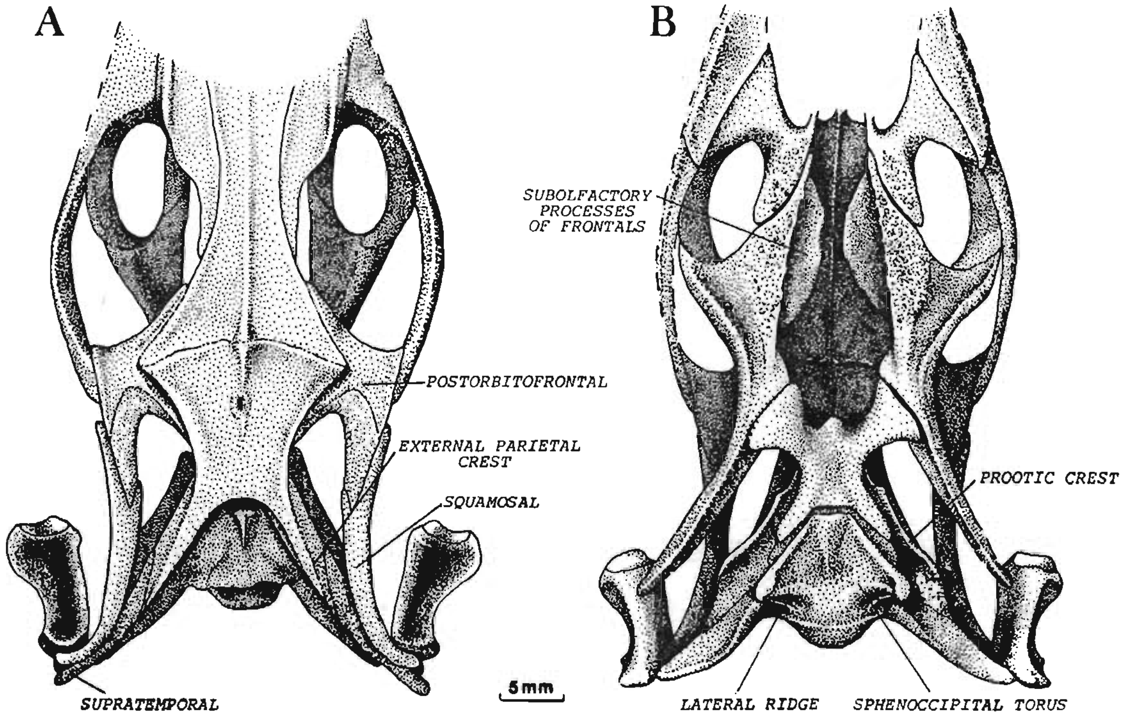


Fig. 15

Telmasaurus grangeri GILMORE, 1943. Skull. A — Dorsal view; B — Ventral view.

Only distal parts of the jugals are preserved. They are laterally flattened and articulate with lateral surfaces of the prefrontals. The postfrontal is almost fused with the postorbital, the traces of the sutures being occasionally preserved as shown by two specimens known to date. At the specimen ZPAL MgR-I/65, the suture is to be seen dorsally on the left (fig. 15).

The squamosal is very long, rounded in transverse section except for its anterior part overlapped dorsally by a flattened posterior process of the postorbital. It is curved laterally concave and has no dorsal process. Its posterior half converges, then parallels the bilaterally flattened blade of the supratemporal adhering to the posterolateral extension of the parietal. Posteriorly, both the squamosal and the supratemporal curve ventrolaterally to reach the incision between the dorsal quadrate condyle and the tympanic crest.

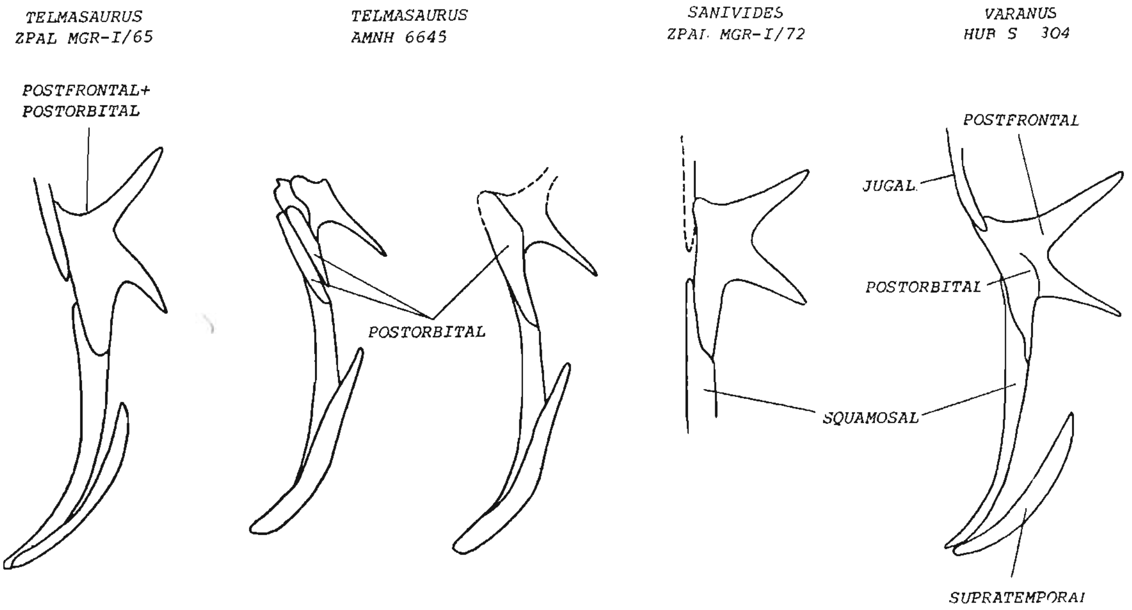


Fig. 16
Structure of the supratemporal and postorbital region in the Varanidae. Not to scale.

Palatal complex. The palatine contacts the maxilla by a flat and distally large maxillary process. This process contributes, along with the ectopterygoid, to separate the maxilla and the jugal from the bordering of the suborbital fenestra. The main body of the palatine is short, flat and horizontal, but the posterior wall of the choana is quite vertical. The vomerine process is very narrow and well individualized. The pterygoid process is covered by numerous small denticles and has an oblique medial border for the articulation with the pterygoid. A broad, triangular palatine process of the pterygoid produces a fairly long but tapering process for this articulation which is obviously a regressive part of the pterygoid. The main part of the palatine process is a dentiferous oval surface which is separated from the ventrally projecting lateral border of the ectopterygoid process by a concavity. The quadrate process is triangular in transverse section. Its axis is strongly bent relative to the main axis of the palatine process.

The ectopterygoid is a dorsoventrally flattened semilunar bone bridging the gap between the pterygoid and the maxillary process of the palatine. The quadrate has both tympanic and medial crests. The tympanic crest is englarged in its inferior part. Between the dorsal condyle and the medial crest is a deep notch.

Occipital segment. The sphenoccipital suture of the trapezoidal type is very loose at the specimen ZPAL MgR-I/65 and thus the posterolateral extensions of the parasphenoid do not adhere to the anterior margin of the sphenoccipital tubercle as they probably did in life. However, they are rather short and do not probably reach very far towards the tops of these tubercles. Each of them is supported by a longitudinal swelling of the prootic instead.

It overlaps this swelling from the ventrolateral side. Both the parasphenoid extension and the underlying swelling separate the ventral surface of the basisphenoid+parasphenoid from the recessus vena jugularis thus replacing a ventrolateral crest that is no longer necessary and, thus, missing. The basipterygoid processes have long and fairly massive stalks and strongly broadened articular ends curving dorsally in their anterior parts; they extend anterolaterally. The sphenoccipital tubercles are situated at the level of about the midlength of the basioccipital and extend ventrolaterally, their thickened tops, made of epiphyses, facing ventrally. Very distinct sphenoccipital toruses extend towards the center of the occipital condyle. The surfaces of insertion of the rectus capitis anterior face posteriad. The lateral ridge, which is very strong in ZPAL MgR-I/65, and tuberal crest may be recognized as two margins, the medial and the lateral one respectively, of a long process of the exoccipital fused to the posterior margin of the sphenoccipital tubercle (comp. fig. 21 D and pl. 9 : 1 c). The second process of the exoccipital, originating from a more dorsal part of the exoccipital extends, as it usually does, towards the prootic to separate the tympanic recess from the foramen ovale (pl. 10 : 1 b, 1 c, fig. 4 G). Directly posteromedially of it is a vagus foramen and posteromedial of the latter is a small hypoglossal foramen. A very broad, low and strongly convex occipital condyle bears no traces of tripartition. Its lower margin passes laterally into a crest extending just over the above mentioned foramina and turning into a sharp ventral margin of the paroccipital process (pl. 9 : 1 c). The part overlying the foramina is exactly the same as a small crest which usually gives to the vagus foramen its semilunar appearance. The paroccipital processes are very long and bilaterally flattened. The main part of the medial (i. e. posterior) surface of this process faces posteriorly and is separated from the upper part, facing dorsally, by a crest continuous with the upper margin of the occipital foramen (see fig. 21 D). As usual, the lower part of the surface of the paroccipital process is presumed to have received the obliquus capitis and the longissimus cervicis, whereas rectus capitis posterior inserted on the upper part. The supraoccipital is only slightly ascending anteriorly, so that the brain case remains rather low. A weak sagittal crest extends along the supraoccipital. Just lateral to it the anterior border of the brain case produces paired processes to articulate with the parietals. These processes are very much like those in *Varanus* but less developed.

The prootic is very long with a long anteriorly spreading alar process separated from the inferior process by a deep trigeminal notch. Extending along the anterior border of the alar process is an alar crest fading at the level of the anterior semicircular canal. The base of the prootic crest begins with the posterior margin of the basipterygoid process, then follows the inferior margin of the inferior process and, finally, the course of the horizontal semicircular canal. The latter is directed to the dorsal corner of the paroccipital process. The prootic crest spread laterally and then ventrally to overhang a recessus vena jugularis.

Family **Lanthanotidae** STEINDACHNER, 1878

Revised diagnosis. — Platynotan lizards with parietal large and flat between laterally situated surfaces for mandibular adductors. No supratemporal arcade. Tendency to lengthening of parietal and to shortening of frontals as well as to elimination of metakinetic mobility. Orbits tending to decrease, prefrontals and postfrontals embracing them from the dorsal side. Parietal foramen tending to disappear. Teeth subpleurodont with basal fluting tending to complication. Tendency to development of intramandibular joint; coronoid eventually contacting the splenial only by a corner. Skull long, suboval in outline, small size. No osteodermal covering fused to skull surface. For remaining characteristics see MCDOWELL and BOGERT (1954).

Table 4

Dimensions of skulls of *Saniwides mongoliensis, Telmasaurus grangeri* and *Cherminotus longifrons* in mm

Species and ZPAL cat. nos.	*Saniwides mongoliensis* MgR-I/72	*Telmasaurus grangeri* MgR-I/65	*Cherminotus longifrons*	
			MgR-III/59	MgR-III/67
Skull as whole				
Condylo-basal length	43	—	22	—
Total length	ca. 46	—	—	—
Length of posterior skull unit (or maximum parietal length)	ca. 13.5	28	9.5	—
Length of snout unit	32	24.4	13.1	—
Length of external nares	e. 9	—	5.8	—
Maximum width over premaxillary	7	—	5	—
Maximum width over jugal arches	—	ca. 28	—	—
Width of postorbital region	11	21.5	—	7.1
Maximum overall width	e. 26	33.2	—	13
Posterior depth	ca. 11.5	9.9	4.9	ca. 4.5
Depth anterior to orbits	5	ca. 5.5	3	—
Frontals				
Sagittal length	18.5	ca. 20.3	7.9	8
Anterior width	5	6.5	2.8	3.1
Posterior width	13	15.7	5	6.1
Minimum width (about the middle)	6	6.3	3.2	3.2
Parietals				
Sagittal length	ca. 8.1	12.5	5.6	6.1
Maximum length	14.5	26	e. 9	—
Minimum width	6	6	3.4	3.8
Minimum distance between external parietal crests	ca. 4.5	5	ca. 2.4	2.5
Maximum posterior width	—	ca. 23	—	—
Brain case				
Posterior depth (metakinetic joint to ventral surface of the occipital condyle)	8.5	10	ca. 4.3	—
Length in ventral aspect (occipital condyle to the basis of anterior parasphenoid process)	11.5	17.9	5.6	5.6
Distance between paroccipital processes	18.5	26	8	8.2
Vomer				
Maximum length	13.5	—	7	—
Maximum width	2.5	—	1	—
Quadrate				
Length of shaft	9	e. 12	5.2	5
Width of distal condyle	4.8	ca. 4.5	1.4	ca. 1.6

Genus *Cherminotus* gen. n.

Holotype: *Cherminotus longifrons* sp. n.

Derivation of the name: Chermin is a Polish spelling of the name of the type locality — Khermeen Tsav; *notus* is added to make the name analogous to *Lanthanotus* to suggest a relationship to this genus.

Diagnosis. — A small-sized lanthanotid not attaining 3 cm of skull length with relatively long and slender snout and non-elongated parietal. Parietal foramen present. Vomers relatively long and slender. Teeth number very low. Basal fluting present but not very complicated.

Geographical and stratigraphical range. — Genus monotypic, known from the type horizon and type locality only.

Discussion. — The genus *Cherminotus* proves to belong to the platynotan lizards by having the following combination of character states: the much retracted external nares; a strong development of the subofactory processes; the splenial much shortened posteriorly probably resulting from a development of the jaw hinge; the pointed teeth with folded dentine and an interdental tooth replacement. The degree of the development of these platynotan character states suggests one of the advanced platynotan families. Manifested by a reduction of the upper temporal arch and a simultaneous formation of a continuous bone ring around the orbit, by a union of the prefrontal and the postfrontal, the skull adaptation of *Cherminotus*, connected with the type of kinesis, differs from the adaptation of the Varanidae as well as from that of the „aigialosaurian" group (*sensu* McDowell and Bogert 1954) and points to both the Helodermatidae and the Lanthanotidae. The low and long brain case of *Cherminotus* and the subolfactory processes much stronger in this genus than in the Varanidae support its distinction from the latter family while recalling character states of both the Helodermatidae and the Lanthanotidae. Characters that point directly to lanthanotid relationships of *Cherminotus* are: a lateral position of the adductor origins on the parietals; a brain case well fitted and broadly articulated to the parietals; a supraoccipital extending posteriorly rather than ventrad of the parietal and an important decrease, as compared to a primitive lizard state, of the pterygoid bending at the level of the basipterygoid articulation, a character clearly connected with a type of the skull kinesis. Some differences relative to *Lanthanotus* such as a less elongated parietal and not shortened frontals as well as a less posteriorly shortened splenial overlapping a coronoid much as in *Heloderma* are those of grade. They do not preclude the lanthanotid relationship of *Cherminotus*. At the same time, they obliterate the differences between the Helodermatidae and the Lanthanotidae. This, however, cannot be regarded as a case for any closer relationship of both families within the range of the Platynota. *Cherminotus* tends to prove that the ancestry of the Lanthanotidae should be looked for among small-sized necrosaurian lizards having lost their osteodermal skull covering very early whereas the Helodermatidae should evolved from the well covered medium-sized ancestors. Adaptive types of skull, similar in both families, should evolved independently in these evolutionary lines and subsequent to the divergence of the characters of body size and osteodermal skull covering.

With its trapezoidal sphenoccipital suture, its protruding prootic crest, a preserved parietal foramen, the skull proportions differing from those of *Lanthanotus* and its less folded dentine, *Cherminotus* well represents a more primitive lanthanotid stage relative to *Lanthanotus*. The specificity of the adaptative type of *Cherminotus* as compared to *Lanthanotus* consists in its proportions. The parietal is shorter and the frontals as well as the rostral part of the skull are longer than is the case in *Lanthanotus*. The significant length of the rostral part is manifested by the vomers which differ very much from those of *Lanthanotus* as well as by the length of the nasals. The nasals parallel the prefrontals on a great distance althought separated from them as they do in *Heloderma* and unlike *Lanthanotus*.

Cherminotus longifrons sp. n.

(pls. 2 : 4; 11 : 1, 2, 3; 12 : 1, 2; figs. 4E, 9G, 17)

Holotype: A skull ZPAL MgR-III/59.
Type horizon: Upper Cretaceous, ?middle Campanian, red beds of Khermeen Tsav.
Type locality: Khermeen Tsav, Gobi Desert, Mongolian People's Republic.
Derivation of the name: Lat. *longus* — long, Lat. *frons* — front.

Diagnosis. — Frontal to parietal length ratio is about 1.5 in sagittal axis. Five widely spaced conical teeth in the maxilla.

Material. — The material consists of two damaged skulls and some other skeletal fragments badly preserved.

ZPAL MgR-III/59 — The holotype is fairly well preserved but lacking both posterolateral processes of the parietal, both quadrates, left jugal arch, left lacrimal and the mandible.

ZPAL MgR-III/67 is deprived of its rostral part, almost all of the jugal arches, both posterolateral processes of the parietal and the supraoccipital. Both postdental parts of the mandible are preserved, whereas the dental parts are lost. Both specimens are exactly the same size and very similar to each other.

Measurements. — See Tables 3 and 4.

Description. — **The skull as a whole.** The skull is long, slender and suboval in outline without any strong expansion of the jugal arches. The maximum width over the jugal arches to the width of the premaxillary body is slightly more than 2. The external nares are extended back to the frontals or almost as far. They completely separate the maxilla from the nasal and wedge in between the maxilla and the prefrontal as a narrow slit. The supratemporal arches are reduced. The posterolateral extensions of the parietal are presumed to have been very long on the basis of the position of the distal extremities of the paroccipital processes. They enclose an angle of about 75°. The paroccipital processes are almost laterally directed, the angle between them being estimated 135°. The upper margin of the brain case contacting with the parietal forms a regular rectangle. The supraoccipitoparietal suture is an almost straight line situated in the same horizontal plane as the prooticoparietal sutures and forming angles of about 90° with them. The dorsal surface of the parietal is divided into a large medial part and narrow lateral parts destined for the origins of the mandibular adductor. The skull surface is free from sculpture.

Skull roof. The rostral body of the premaxilla is broader than long. The palatine processes are separated from each other by a deep angular notch and from the outside by small notches. The incisive process is bilobed. It passes into two convexities running divergently along the medial borders of the palatine processes to their tops, which make up articulations with the vomers. The premaxillary foramina are probably absent. The number of teeth cannot be stated. The nasal process of the premaxilla is supposed to be rather long, probably half the length of the external nares. This is based on the morphology of the anterior parts of the nasals which were probably overlapped by this process of the premaxilla.

The nasals are preserved as an imprint in the holotype. They were probably small lozenge-shaped bones passing anteriorly into long slender processes overlapped by the premaxilla. The exposed parts of the nasals were about 0.6 of their entire length. The sagittal suture was probably not fused. As judged from the W-shaped frontonasal suture preserved at ZPAL MgR-III/67, the nasals were separated from the prefrontal by lateral processes of the frontals extending to about the middle of the nasoprefrontal contact. Anteriorly, the prefrontal and the nasal were separated by a slit-like prolongation of the external nares.

The frontals are paired, rather elongated bones having their margins parallel over 2/3 of their length and broadening in their posterior 1/3 only. They are completely excluded from the upper margins of the orbits by a contact between the prefrontal and the postfrontal. The descending processes of the frontals are very large, directed ventromedially but not fused with their fellows beneath the olfactory tracts. They are produced by a whole orbital part of the frontals but attain their largest extension at about 1/3 of their length from the frontoparietal suture. This suture is quite straight, certainly permitting an important amount of motion.

The main body of the parietal is slightly less than 1/3 the length of the frontals but the posterolateral extensions of the parietal are almost as long as the main body. Converging towards the posterior part of the main body external parietal crests meet a straight nuchal crest, thus delimiting a central part of the dorsal surface of the parietal. Its lateral surfaces received the mandibular adductor, whereas its slope, posterior to the nuchal crest, received the neck muscula-

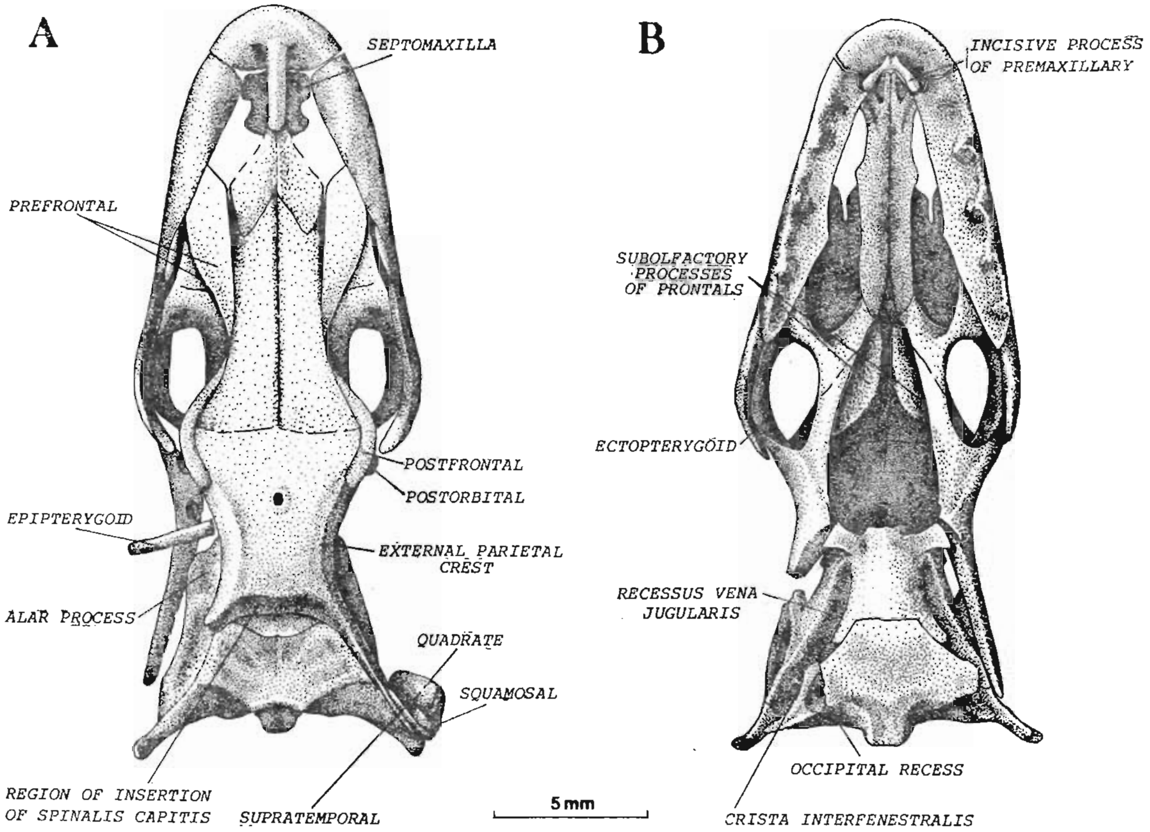


Fig. 17
Cherminotus longifrons gen. n., sp. n. Skull. A — Dorsal view, B — Ventral view.

ture but distinct muscle traces cannot be identified. Lying at about 2/5 of the main body length from the frontoparietal suture is a parietal foramen.

The maxilla is a rather low triangle not extending to the dorsal surface of the skull roof. The anterodorsal margin is straight. Posteriorly, it forms a suture with the prefrontal, whereas anteriorly it turns gently ventromedially to enter the fenestra exonarina. Its contact with the septomaxilla is far from being clear owing to preservation. The process of the maxilla extends some distance beneath the anterior part of the orbit. It faces much more upwards than backwards and is overlain by the lacrimal and the jugal. The palatal shelf of the maxilla is fairly broad but it is much shallower than is the case in *Lanthanotus*. It tapers in its posterior 1/3, while making up a suture with the maxillary processes of the palatine. The maxilla is completely excluded from the bordering of the suborbital fenestra by a palatoectopterygoid contact. The anterior part of the palatal shelf curves gently towards the vomer. It contributes, along with this bone, to the articulation with the prolongation of the incisive process (fig. 17B).

The dorsal surface of the prefrontal is roughly rhomboidal, its two sides being sutured to the maxilla and the frontal while two others contributing to the orbit and external nares. The orbital lamina of the prefrontal projects ventrally from about half the length of this bone. A long and slender supraorbital process extends along 2/3 the length of frontals to meet the postfrontal with its top. The prefrontopalatine suture extends in a horizontal and transverse plane.

The jugal has a strong bilaterally flattened horizontal ramus and a much more delicate anteroposteriorly flattened ascending process loosely touching the postfrontal. Medially it is sutured to the ectopterygoid and anteroventrally to the maxilla. Anterodorsal to the jugal ia a lacrimal but the suture between these bones is not quite clear. Their probable share in this part of the orbital rim is reconstructed at fig. 14E. The lacrimal is a small plate-like bone. Probably only one slit-like lacrimal foramen is situated on the prefrontolacrimal suture.

As seen at the specimen ZPAL MgR-III/67, the postfrontal is merely a narrow bone bar closely adjoining the margins of the frontal and the parietal. There is no jugal process causing the most common triangular shape of this bone, nor is there any trace of the postfrontojugal articulation. Althought the jugal arch seems to have been quite complete, the contact between these bones must have been loose. Posteromedial to the top of the temporal process of the jugal is a rudiment of the postorbital. The squamosal is atrophied. It consists of the posterior part of the anterior process with its downturned top articulating with the quadrate.

Palatal complex. The vomer is very long, slender and ventrally convex in transverse section. The two are sutured in the midline over more than 2/3 of their length. The anterior extremity of the vomer is subdivided by a longitudinal groove into two convexities. The lateral one is sutured to the palatal shelf of the maxilla and to the incisive part of the premaxilla, the medial one enters into the V-shaped excavation behind the incisive process. Taking apart a direct connection between the vomers and the incisive processes present in *Lanthanotus*, the configuration of the bones in this region is very similar in both genera.

Typical of Platynota, the palatine consists of three slender processes distinctly separated from each other. The vomerine process is sutured to the vomer from a posterolateral side. It is connected to the maxillary process only deep in the nasal cavity by means of an ascending lamina constituting the anteroinferior wall of the orbit and suturing to the prefrontal. Confined to this lamina and situated near its lateral border is a horizontal infraorbital canal. The maxillary process is much broadened at its distal end which is sutured to the maxilla. The posterior corner of this part dorsally overlaps the ectopterygoid, which is a rather strong, semilunar bone. The length of the pterygoid process is not known, nor can presence or absence of the palatal teeth be determined.

The palatine process of the pterygoid is a narrow bone bar rather than a triangular plate. As eidenced by a narrow, roughened surface present on its ventral side and similar to a tooth bearing surface in *Lanthanotus*, it probably bore a simple row of teeth. Only posterior to the palatal process the pterygoid broadens laterally to pass into the triangular ectopterygoid process. The distal part of the latter is a delicate perpendicular plate suturing to the ectopterygoid from a posterolateral side. The quadrate process is a deep, medially concave bone bar. The axis of the quadrate process is almost the same as that of the palatine process, there being no abrupt bending of the pterygoid known in many other lizards. This, along with the position of the basipterygoid articulation results in a subparallel position of the pterygoids recalling *Lanthanotus*. Just posterior to the broadened part of the pterygoid, at a dorsal surface of this bone and anterior to the basipterygoid articulation is a rounded columellar fossa. The epipterygoid is a slender bone about 5 mm in length with a broadened dorsal extremity articulating with a lateral part of the parietal.

The quadrate is a slender bone with both a tympanic and a medial crest developed, the first one being stronger than the second. By a resting phase of the jaw apparatus the main axis of the quadrate is almost perpendicular to the skull roof, while curving abruptly backwards in its upper part. The tympanic crest follows this course of the bone, while vanishing near the dorsal condyle. Dorsally, it is shifted forward, its anterior convex surface being the most anterior part of the quadrate. Medial to it, the anterior surface of the quadrate becomes slightly concave and slants posteromedially. The posterior crest is the most strongly curved part of the quadrate. It projects strongly dorsally while flattening out just above the ventral condyle. Its posterior border makes up a semicircle with a retroarticular process of the mandible. It divides the posterior surface of the quadrate into two concave parts. The dorsal condyle faces posterodorsally. It is separated from the tympanic crest by an incision to which the curved extermity of the squamosal is fitted. This condyle articulates medially with the posterolateral surface of the paroccipital process and dorsally with the supratemporal. The ventral condyle is double. Its axis is nearly perpendicular to the long axis of the skull.

Occipital segment. The external surface of the basisphenoid + parasphenoid is evenly convex in transverse section, there being no ventrolateral crests. The sphenoccipital suture is trapezoid in shape but the posterolateral extensions of the parasphenoid do not reach to the tops of the sphenoccipital tubercles. The sphenoprootic suture is incised about the middle of the length of the body to produce the entrace to the Vidian canal. The slim peduncles of the basipterygoid processes extend almost directly laterally and almost horizontally. A rounded and swollen ventral part of the basioccipital passes into a rather long and laterally directed sphenoccipital tubercle and into the occipital condyle which is slender and projecting far posterior. Their tops being damaged, it is impossible to determine their shape and the exact position of the occipital recess. The sphenoccipital torus is not developed, the medial surface of the sphenoccipital tubercle being evenly convex. The posterolateral parts of the basioccipital curve gently upwards to contribute a lower part to a fossa for the rectus capitis anterior. Extending from the ventrolateral part of the foramen magnum towards the top of the sphenoccipital tubercle and bordering this fossa from the dorsal side, is a distinct, much protruding lateral ridge produced by the exoccipital. Corresponding to a great lateral extension of the sphenoccipital tubercles, a lateral ridge and a fossa for the rectus capitis anterior as well as the whole medial plate of the exoccipital are all laterally expanded. The fossa for the rectus capitis anterior faces posteroventrally. Superior to the lateral ridge is a semilunar fissure perforated for the nerves X—XII (no other foramina being present medial to it). The posterior surface of the paroccipital process is separated from the dorsal surface by a ridge in continuation with the upper margin of the foramen magnum. The distal extremity of the paroccipital process strongly projects ventrally. The anterior wall of the paroccipital process is distinctly subdivided into the upper part overlapped by the prooticum and the lower one facing ventrally with a slight anterior inclination. The ridge making up a limit between these parts is directed to the point intermediate between the upper and lower corner of the distal extremity of the paroccipital process. The presence of a ventral surface instead of a ventral border is a difference relative to the paroccipital process of *Lanthanotus*. However, as regards the inclination of this surface, *Cherminotus* represents an intermediate stage between the primitive horizontal position and advanced vertical one. The posteroventral border of the paroccipital process passes medially into an almost vertical crista tuberalis. As usual, it gives off a long process bearing a crista interfenestralis separating the occipital recess from the foramen ovale.

The prootic crest (see fig. 4E) extends a distance apart from the horizontal semicircular canal, first subparallel then converging with it. It starts from beneath the inferior process and extends posterodorsally. Behind the anterior semicircular canal its course changes into posterolateral. Beginning with the level of the sphenoccipital tubercle it turns towards the upper part of the distal extremity of the paroccipital process but does not reach it. The posteroventral prolongation of the alar crest bordering the trigeminal notch from above converges with the prootic crest vanishing about the middle of the length of the prootic. The part of the prootic situated above the external semicircular canal faces upward and contributes to the lateral part of the brain case roof. It is developed forwards to pass into the extensive alar process. This process slopes ventrolaterally. The part of the prootic situated between the external semicircular canal and the prootic crest (not present in *Paravaranus*) makes up an important part of the lateral wall of the brain case. The recessus vena jugularis is a shallow and narrow furrow running from the entrance of the Vidian canal to the concavity of the foramen ovale. Posterolateral to this foramen it passes into the triangular lower surface of the paroccipital process, differing from the jugular fossa of *Lanthanotus* which passes into the anterior surface of the paroccipital process.

The mandible (fig. 9G). In the specimen ZPAL MgR-III/67 the anterior halves of both manibles are missing. The breakage on both occurred at the same point anterior to the coronoid, the surangular and the prearticular. The bone margins seem to be natural, only the angular being broken. This is suggestive of the development of the intramandibular jaw hinge of the platynotan type but the line of joint is not straight. The supraangular and the medial part of the coronoid reach further than the lateral part of the coronoid, whereas the prearticular is posterior to a suture between the supraangular and the dentary. The postcoronoid ramus is long and low and shows only a slight sigmoid curvature. Judging from the sp surface (see fig. 29) on the coronoid, its anterior ramus was overlapped by the splenial, as reconstructed in fig. 9G', instead of having a brief contact with it as is the case in *Lanthanotus* (fig. 9H'). Thus, it represents a standard derived platynotan character state. The much projecting apex of the coronoid is situated quite posterior of the coronoid body. The medial surface of the coronoid is concave and deeply incised ventrally.

The supraangular is a large laterally flattened bone. Its long axis is straight, only the posterior part being produced medially, immediately in front of the glenoid. On the lateral side of this part of the manible there are three foramina. Two of them, situated beneath the anterior and the posterior part of the coronoid respectively, are probably two parts of the doubled anterior supraangular foramen. The third one, a posterior supraangular foramen, is situated just anterior to the glenoid.

The angular is a narrow bone constituting the lower border of the mandible exposed but very little at its both sides. It probably reached more anterior than the level of the supposed jaw hinge and posterior to about half a length of the postcoronoid ramus. The prearticular was probably covered medially by the splenial up to the level of the posteroventral corner of the anterior ramus of the coronoid (see fig. 19G'). The mandibular fossa is narrow and slit-like. The suture between the prearticular and the supraangular cannot be traced owing either to a fusion of the bones or to the state of preservation.

The retroarticular process is a subrectangular, rather long bone curving neither medially nor ventrally. Its lower surface passes gradually into both lateral and medial surfaces of the mandible.

As evidenced by a fragmentary mandible of the specimen ZPAL MgR-III/59, the dentary is rather massive, its depth rapidly increasing posteriad. It has a largely opened Meckalian groove. The tooth bearing margin is very broad without any trace of a subdental ridge. It projects strongly to the medial side and is supported ventrally by a slightly convex wall turning anteriorly into a slightly concave dorsolateral wall of the Mackelian fossa.

Dentition. The teeth are subpleurodont, conical in shape with largely extended bases and pointed tops. They are widely spaced and firmly ankylosed to the tooth bearing bones. The tooth replacement is alternate. There are 5 teeth in the maxilla and the number of tooth positions is 8. Basal fluting is hardly recognizable but probably developed as judged from the character of the weathered surfaces of the teeth.

PHYLOGENETIC CONCLUSIONS

A wider or narrower range may be ascribed to the infreorder Anguimorpha depending on whether primitive lizards, referred to as Preanguimorphan grade, or any of them, are included into it or not. This problem is not definitively solved in the present paper although a speculative dendrogram (fig. 19) suggests the first possibility. No matter whether the preanguimorphan lizards really belong to this infraorder, the Anguimorpha may be viewed as a basically predacious lizard line. Although the dentition is mostly of non-predatory type in the Diploglossa, the intermediate (RIEPPEL 1978) type of tooth replacement they usually display is not phylogenetically independent from the varanid pattern of the purely predatory platynotan but is believed to result from the same initial cause. It is argued here that the increase of tooth spacing, which added to sectorial efficiency of the dentition, initiated this evolutionary sequence. A migration of successive teeth towards and into the interdental spaces, which was equal to transformation of the primitive iguanid type of tooth replacement into the varanid one via the intermediate type, was a direct result of the increased spacing of teeth. The less derived, intermediate tooth replacement which should be regarded as a shared and derived character state in both superfamilies, was probably very variable and could easily be reversed into the more primitive condition as was the case in some Diploglossa, or developed into a more derived pattern.

In the case of inclusion of the preanguimorphan lizards into the range of Anguimorpha, a widely spaced dentition should be regarded as the only new structural character state they acquired. If the preanguimorphan lizards are excluded from the Anguimorpha, the complex of characters ancestral to the latter would also include brain case structure, which is the most important feature undergoing a change at the boundary between the Preanguimorphan and Necrosaurian grade. The ancestor of the Anguimorpha would thus be characterized by a rather complex composition of tooth and brain case characters. Even so, such a complex of characters has probably developed gradually, the process being much extended in time.

The brain case structure was quite primitive at the Preanguimorphan grade. The brain case characters which are considered shared and derived in two main lines of modern Anguimorpha, the Platynota and the Diploglossa, include a long, anteriorly expanded alar process, a trapezoidal sphenoccipital suture, recessus vena jugularis extending more vertically than horizontally and proportions that give a long and low aspect to the brain case. Although some of these character states may prove to be developed in parallel, the general structure of the brain case of the common ancestor of the Platynota and the Diploglossa must have been much advanced in this direction. Having developed their modern brain case structure, or a predisposition to its development, the ancestors of the main anguimorphan lines certainly merit separation as a distinct morphological grade, i. e. early anguimorphan grade, which is not recognized here because is not represented in the present material. The anteriorly shortened splenial as well as a tendency to increase of the mesokinetic mobility (resulting in a straightening of the frontoparietal suture) and development of subolfactory processes were probably also characteristic of this evolutionary grade.

An important evidence concerning the time of existence of the common ancestor of the Platynota and the Diploglossa is given by the Late Jurassic (Portlandian) *Dorsetisaurus purbeckensis*, the best known of the earliest representatives of the infraorder, displaying a quite modern type of the brain case, which is, thus, considered a representative of the early anguimorphan grade. The hypothesis preferred in the present paper, that the osteodermal skull covering had not developed a definite shield pattern in the common ancestor of both superfamilies (fig. 28A) suggests that *Dorsetisaurus*, which has this pattern developed, was already divergent on the diploglossan line. Although this genus differs from the Diploglossa in its dorsal adductor attachment, considered varanoid by HOFFSTETTER (1967), this character state is probably primitive in the whole anguimorphan stem as are the predaceous habits with which the muscular attachment is correlated. The separation of the Platynota and the Diploglossa must have been prior to the time of existence of *Dorsetisaurus*. It probably occurred about the Middle Jurassic, the more so that the definite platynotans, the Aigialosauridae, appeared in the fossil record as early as the Early Cretaceous or even earlier (*Proaigialosaurus*, Late Jurassic; KUHN 1958).

The phylogeny of the Platynota is here interpreted as extensively resulting from parallel evolution. This is inferred from the mosaic pattern of character complexes of platynotan groups. The consistency of the pattern implies close relationships of the groups compared whereas the mosaic composition of character complexes indicates that most of the character states

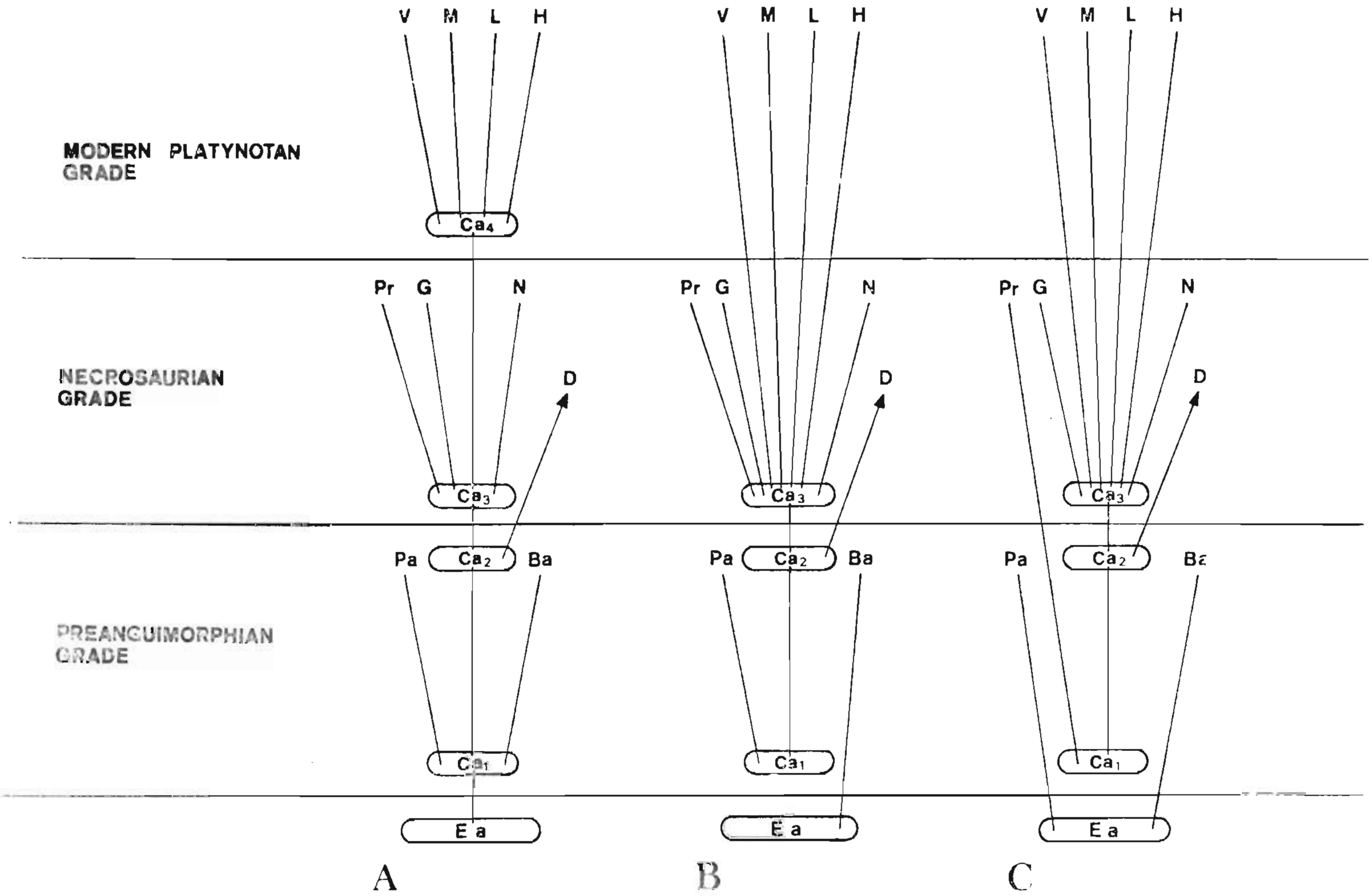


Fig. 18
Three models of phyletic relationships between lizards of different morphological grades of anguimorphan evolution. Note the monophyletic origin in (B), (C) and the diphyletic origin of the necrosaurians in (C). Ba — Bainguidae; Ca — common ancestor of *1* Anguimorpha, *2* Platynota and Diploglossa, *3* Platynota, *4* modern platynotan lizards; D — Diploglossa; Ea — Early autarchoglossa; G — Gobiderma; H — Helodermatidae; L — Lanthanotidae; M — Mosasauridae; N — Necrosauridae; Pa — Paravaranidae; — Pr — Proplatynotia; V — Varanidae.

were not developed but only forshadowed in the common ancestor and that they, consequently, may not be regarded as synapomorphies.

The phylogeny of the Platynota is, thus, characterized by the development of grades corresponding to two adaptative levels. One, characterized by the absence of a functional intramandibular and of a hypokinetic joint, by a well developed osteodermal skull covering and unretracted external nares, is a necrosaurian grade and the second one, having all these characters developed to a more derived state and usually displaying a tendency to gigantism, is a modern platynotan grade. The phylogenetic relations between these grades, as well as that between the necrosaurian and preanguimorphan (or early anguimorphan) grades, may be viewed as strictly monophyletic (fig. 18A), polyphyletic (fig. 18C) or intermediate (fig. 18B). The importance of parallel evolution in the phylogeny of Anguimorpha points more to one of the two latter models than to the first one. The problem is tentatively resolved as follows.

The necrosaurian grade is regarded as a monophyletic group the ancestor of which improved its predatory adaptations by increasing its kinetic skull mobility (corresponding structural changes affecting palatines and skull sutures, first of all pterygopalatine and frontoparietal suture) as well as by tending to attain a lateral mobility of mandibles by loosening the sutural connections between the mandibular bones. Having acquired such generalized predatory advantages the necrosaurian ancestor must have penetrated different ecological niches that were characterized by adaptation to different pray. This resulted, first, in a variable increase of size and then in a differentiation of the osteodermal skull covering. The monophyletic approach to the necrosaurian origin is called into question by only one form, *Proplatynotia*. Its brain structure which is supposed to be rather primitive, as regards the absence of the alar process at least, indicates that it diverged from the common stem before its subdivision into the platynotan and diploglossan line. The similarity of the adaptation of *Proplatynotia* to that of other necrosaurians, along with the somewhat equivocal character of the data concerning the brain case in this genus (see. pp. 26, 34) indicates that the independent development of *Proplatynotia* from the preanguimorphan stem (comp. fig. 7B) is rather doubtful.

The lizards informally called the modern platynotans are still more strikingly uniform than the necrosaurian lizards. However, the mosaic pattern of their structure is more accentuated too (Table 5), which makes it difficult to derive them from a common necrosaurian ancestor. The consistency of this group partly consists in parallel evolution, i. e. in the uniform ancestral pattern and a similar direction of adaptation toward increase of efficiency of predatory ability. The most significant tendency is formation of a hypokinetic axis within the skull floor which leads the skull kinetic mechanism to a more derived state. Parallel to development of mesokinetic mobility, metakinesis is becoming reduced (see p. 86). Retraction of the external

Table 5

Distribution of states of some characters in modern platynotan groups

Analyzed taxa Characters	Helodermatidae	Lanthanotidae	Varanidae	Mosasauridae	Hypothetical common ancestor
Pterygopalatine suture	○	○◑ ?	◑	○	●
Dentine folding	○	○	◑	○	●
Subolfactory processes	○	○	○	●	●
Intramandibular mobility	○	○	●	○	○
Retraction of internal nares	○	○	○	○	○
Retraction of external nares	○	○	○	○	○
Body size	○	●	○	○	●
Skull covering	●	○	○	○	●

● — primitive state, ○ — derived state, ◑ — derived state only in some representatives of a given group, primitive in others.

nares, which attains its climax at this evolutionary level, is hypothesized to be a consequence of a process initiated at the necrosaurian grade and namely of the retraction of internal nares. Formation of the intramandibular joint is, as well, a continuation of an earlier tendency that attained its climax only in some modern platynotan lines.

A polyphyletic pattern of evolution of this group is supported by the Late Cretaceous representatives, *Cherminotus* and *Saniwides* (Lanthanotidae and Varanidae respectively). They are much more primitive than the extant representatives of these families but are decidedly engaged in the corresponding evolutionary lines and thus do not obliterate the differences between the families to indicate their common ancestry. *Saniwides* may even be regarded as a varanid morphologically intermediate between the necrosaurian and the modern platynotan grade.

GENERAL PART

The skull structure is here considered as being formed by three parts differing from each other by their morphology, their functions and the factor complexes they depend on. These are: the occipital segment and the maxillary segment, which are two main units of the kinetic skull apparatus named by VERSLUYS (1912), and the osteodermal skull covering — a secondary dermal bone deposited over the dermal skull roof. Both the maxillary segment and the osteodermal skull covering are directly connected with the adaptation to environmental factors from which the occipital segment is more separated. The last one displays much less variability and its connection with the presquamatan evolutionary stage is much clearer. Its use in taxonomy inferior to infraordinal level is very limited, the same simple evolutionary processes being repeated in different lines.

The type of osteodermal skull covering is dependent on its protective function and on kinetic skull mobility affecting the skull roof, both these qualities being subject to a differentiation in saurian phylogeny. They both are important to taxonomy at about the familial level and so is the osteodermal skull covering to a certain extent. However, the simplicity of the ontogenetic development of the osteodermal skull covering (see p. 90) and its dependence on simple mechanical rules may cause homeoplasy of its states, thus reducing its taxonomic value at the suprageneric level.

The maxillary segment is more directly dependent on kinetic skull activity related to feeding than is the osteodermal skull covering, and is, thus, the most relevant to taxonomy at the familial and suprafamilial levels. A second function that has much bearing on the structure of maxillary segment is perception, which influences orbits and nares and contributes to the taxonomic value of the complex of characters of the maxillary segment.

Occipital segment

Brain case floor and sphenoccipital suture

The anterior element contributing to the floor of the brain case consists of two superimposed bones, a basisphenoid and a parasphenoid. These elements being tightly fused, they have been sometimes (SIEBENROCK 1892, OELRICH 1956) referred to as an entity called a basisphenoid and provided with an anterior parasphenoid process (a cultriform process). But its double nature and the mutual relations of both elements have already been recognized by GAUPP (1910), LAKJER (1927) and then by VAN PLETZEN (1946) and JOLLIE (1960) in juvenile skulls of *Anguis*, *Lacerta*, *Iguana* and *Cordylus*. The shape of this double element is quite consistent

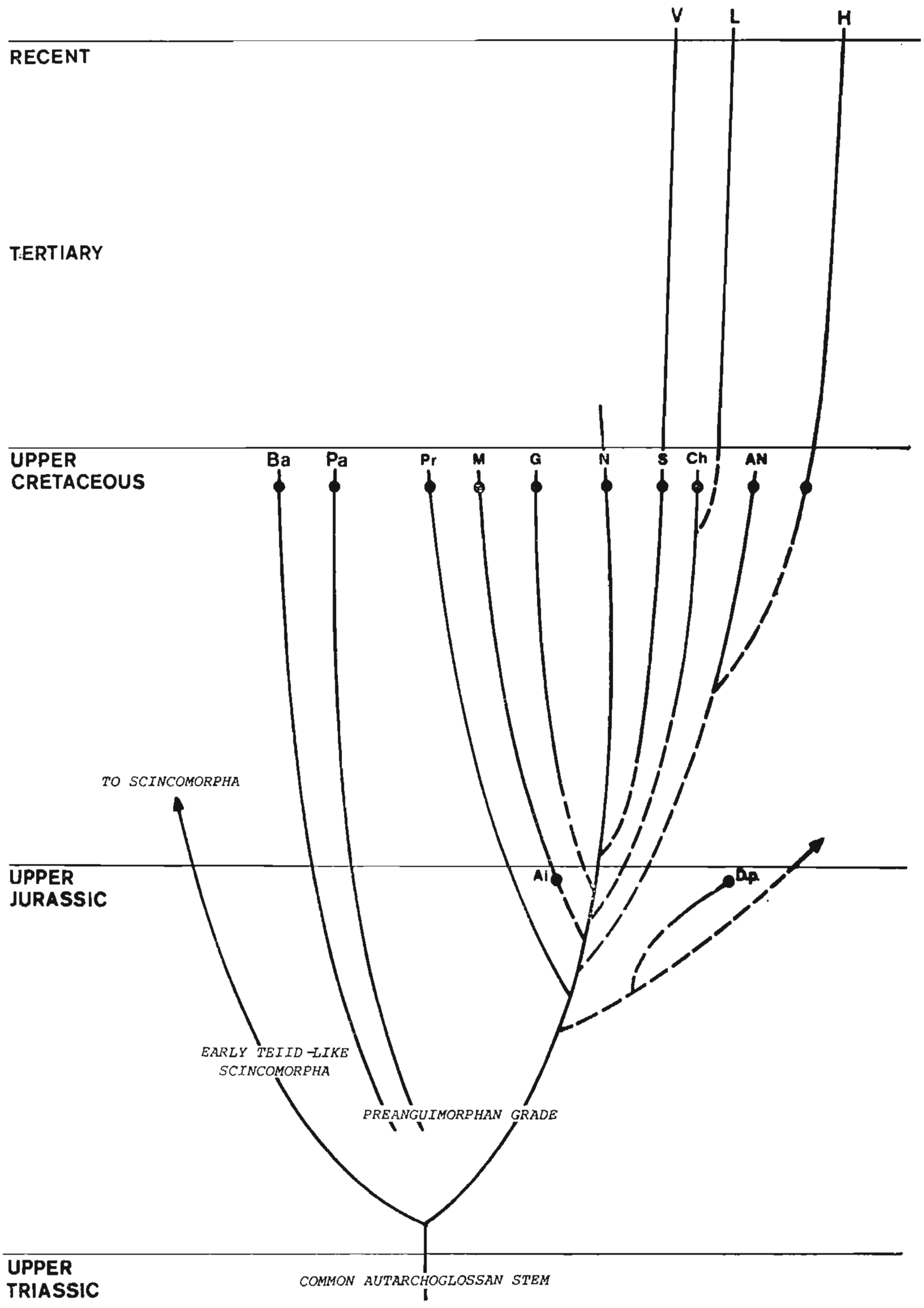


Fig. 19
Speculated dendrogram of Anguimorpha. Main pretertiary fossil records and extant occurrences denoted by points. Ai — Aigialosauridae, AN — American necrosaurians, D. p. — *Dorsetisaurus purbeckensis*, S — *Saniwides* and *Telmasaurus*. For other explanation see figs. 18 and 28.

within Anguimorpha, almost all of the Late Cretaceous genera of the fauna described as well as a quantity of extant genera such as *Anguis*, *Ophisaurus*, *Abronia*, *Xenosaurus*, *Heloderma* and Upper Jurassic *Dorsetisaurus* (HOFFSTETTER 1967, fig. 12) displaying the same pattern. The parasagittal part of the parasphenoid+basisphenoid contacts the basioccipital about half the length of the brain case floor, whereas its lateral parts reach much further backwards down the anterior surface of the sphenoccipital tubercles. The resulting suture is trapezoidal in shape, its parasagittal part extending straight transversally and the lateral ones being directed posterolaterally (fig. 20A—E). Running from the posterodistal corners of the basipterygoid processes up to the posterior extremities of the posterolateral extensions of the bone are usually distinct ventrolateral crests separating a flattened ventral surface of the sphenoid part of the brain case from its lateral surfaces.

As demonstrated by young skulls (*Heloderma*, and *Anguis*, pl. 4 : 4), the posterolateral parts of the sphenoid part of the brain case pertain to the bony lamina overlapping the body of the bone ventrolaterally and so, are clearly parts of the parasphenoid (the basiparasphenoid of JOLLIE 1960). They turn up to overlap the lateral walls of the brain case floor and give the extensions to the posterior and dorsal parts of the basipterygoid processes to produce the lateral walls of the Vidian canals. The presence of distinct lateral parts of the parasphenoid perfectly corresponds with a tripartite structure of this bone observed by GAUPP (1910) and LAKJER (1927). Whether or not the basisphenoid is covered ventrally by a central part of the parasphenoid (rostroparasphenoid of JOLLIE 1960) is far from being clear. If it is, the parasphenoid probably reaches to the transverse part of the trapezoidal suture and is completely fused to the basisphenoid. The basisphenoid usually contacts the basioccipital by means of paired, flat condyles directed posteriorly and appearing at the ventral surface of the brain case floor as two eminences.

The basioccipital is a regular hexagon with two bases directed transversally. These are: the suture between the basisphenoid and the basioccipital part of the occipital condyle. Two lateral apexes of the hexagon are produced by the sphenoccipital tubercles. Both anterolateral sides are overlapped by the posterolateral extensions of the parasphenoid, whereas the posterolateral sides are sutured to the exoccipital. The sphenoccipital tubercles are variously shaped but usually trihedral, owing to the medial wall being subdivided into the anterior and posterior parts. Extending from the top of the sphenoccipital tubercle medially or posteromedially up to the midpoint of the occipital condyle is a convexity separating these parts. It is an anterior limit of attachment of the rectus capitis anterior which will be referred to as a sphenoccipital torus (see. fig. 20ox). The posterior part of the sphenoccipital tubercle along with its posterolateral border called crista tuberalis (OELRICH 1956) are produced by the exoccipital. The apex of the sphenoccipital tubercle and a part of its lateral surface is made of an independent bone a type of epiphysis, often completely fused with the basioccipital. Superior to this bone the lateral wall of the sphenoccipital tubercle is hollow for the occipital recess housing a terminal part of the perilymphatic duct (fenestra cochlearis of JOLLIE 1960).

It was claimed by GOW (1970) that the basisphenoid has not reached the basioccipital in Eosuchia, the parasphenoid having bridged the gap and overlapped the anterior part of the basioccipital. This type of structure is suggested by GOW to represent the Upper Permian level of development of the diapsid skull, a long parasphenoid and a short basioccipital being probably characteristic of saurian ancestors. Since the share of the occipital and sphenoid components

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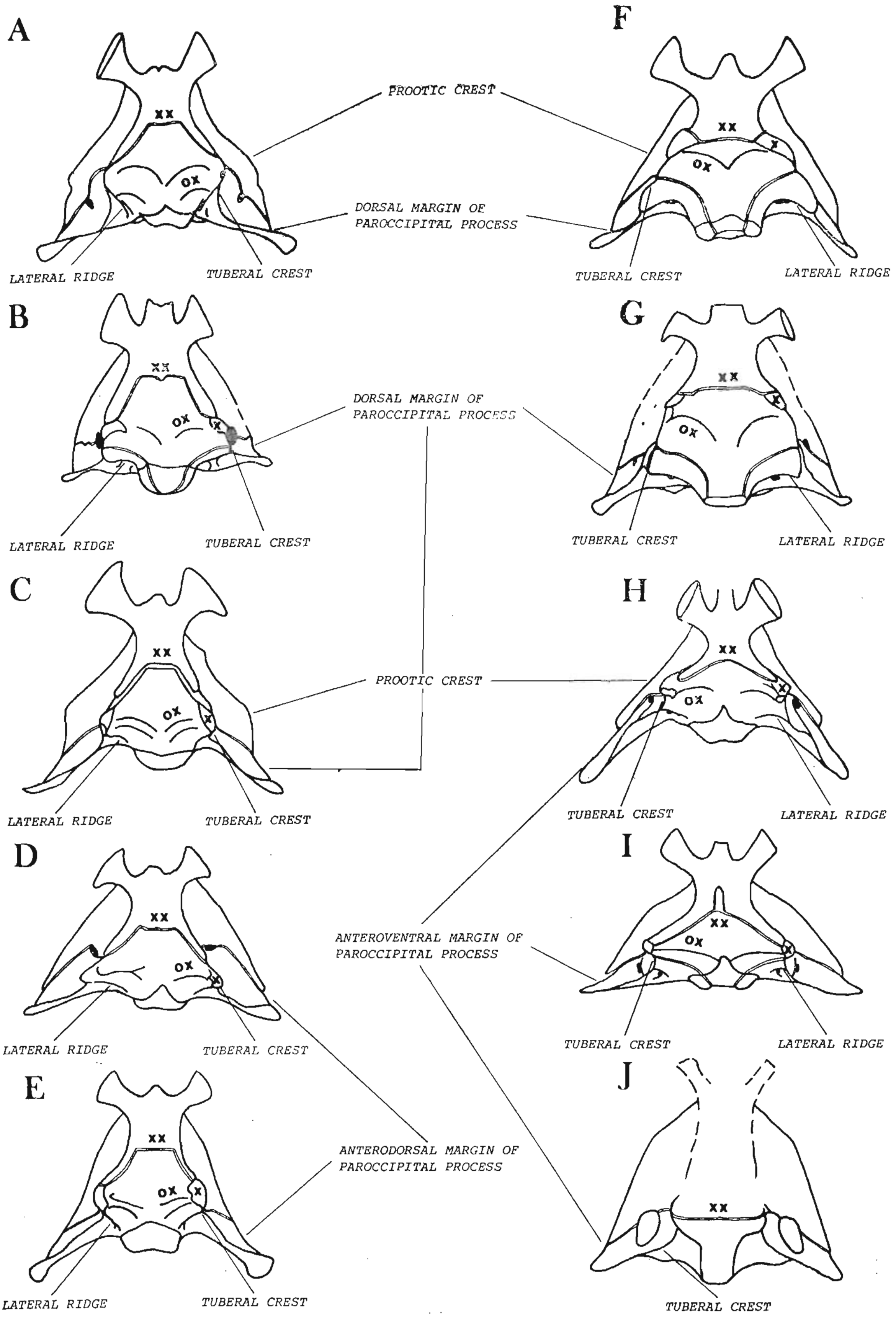
Fig. 20

Brain case structure in Sauria. Ventral view. A — *Xenosaurus grandis* MCZ 46785; B — *Anguis fragilis* ZPAL R-I/5; C — *Telmasaurus grangeri* ZPAL MgR-I/65; D — *Gobiderma pulchra* ZPAL MgR-III/64; E — *Saniwides mongoliensis* ZPAL MgR-I/72; F — *Varanus griseus* HUB S. 304; G — *Lanthanotus borneensis* MCZ 8305; H — *Physignathus lesueuri* ZPAL R-I/1; I — *Paravaranus angustifrons* ZPAL MgR-I/67; J — *Bainguis parvus* ZPAL MgR-II/46; x — epiphysis of sphenoccipital tubercle; xx — sphenoccipital suture; A—E trapezoid type, F, G derived, shortened type, H, J angular type; ox — sphenoccipital torus. Not to scale.


A
xx
ox
LATERAL RIDGE
TUBERAL CREST
PROOTIC CREST
DORSAL MARGIN OF PAROCCIPITAL PROCESS
F
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TUBERAL CREST

in the brain case floor is about the same in almost all lizards, its changes must have proceeded very early in their phylogeny. However, the differences in types of sphenoccipital sutures, to be seen between saurian infraorders, resulting from different rates and methods of shortening of the parasphenoid as well as from its differentiated shape, indicate that this process has been subsequent to the main divergence of the suborder.

The parasagittal part of the parasphenoid (the rostroparasphenoid of JOLLIE 1960) was usually the first to be shortened while leaving the unshortened lateral extensions. The latters could follow the central part only later on, resulting in a more derived short condition (fig. 20 F, G). The posterolateral extensions of the parasphenoid could be widely separated by a straight sphenoccipital suture of trapezoidal type (fig. 20 A—E) or could they more or less converge eventually producing an angular suture (fig. 20 H, J). The trapezoidal suture is regarded to be a shared derived character state of anguimorphan lineages, some representatives such as *Varanus*, *Lanthanotus*, *Gerrhonotus* having developed, independent from one another, a more derived shortened condition. The trapezoidal suture is paralleled by many Scincomorpha (some Gerrhosauridae, Teiidae and Scincidae), their type differing by a more dorsal position, more convergent course and usually more shortened state of the posterolateral extensions of the parasphenoid. Some representatives of this shortened type imitate the angular type of suture characteristic of Iguania (fig. 20 H), which does not occur in Anguimorpha. In any case there is an important but not full overlap of ranges of variability of this character between Anguimorpha and Scincomorpha. The trapezoidal type of suture is always correlated with the sphenoccipital tubercles lying about the mid-length of the basioccipital. Their position being directly connected with the action of flexors of the altantooccipital joint (the rectus capitis anterior), the type of mobility of this joint seems to be very stable in both infraorders. It is seriously changed in advanced Platynota only: in the modern Varanidae (but not in *Saniwides*, *Saniwa* and, according to MERTENS 1942, figs. 227, 231, in some representatives of *Varanus*) as well as in the modern Lanthanotidae, both groups having achieved a similar condition independently (fig. 20 F, G). Here the sphenoccipital tubercles are shifted to the level of the suture between the basisphenoid and basioccipital and the posterolateral extensions of the parasphenoid are correspondingly reduced. Posterior to the sphenoccipital torus is a muscular attachment surface for the rectus capitis anterior. In *Varanus* and *Lanthanotus* it faces ventrally rather than posteriorly and increases at the expense of the length instead of height, thus the sphenoccipital tubercles do not protrude ventrally.

The Diploglossa show a tendency to elongation of the basioccipital relative to the basisphenoid. This is a more derived state connected with the elongation of the whole posterior part of the skull in this group.

Exoccipital

The exoccipital (fig. 21) is completely fused with the opisthoticum. This compound bone (the occipital of JOLLIE 1960) consists of a medial subquadrangular posteriorly facing plate and a stout paroccipital process extending laterally. The medial part is sutured to the posterior margin of the basioccipital ventrally, its lateral margin is a tuberal crest and the medial one contributes to the occipital condyle and the lateral margin of the foramen magnum. The paroccipital process extends from the upper part of the medial plate, its ventral margin making usually an angle of about 90° with the tuberal crest. The medial part of the bone bears foramina for the nerves X+XI and XII. A laterally concave semilunar fissure which is an isolated part of the metotic fissure was an exit of the vagus and accessory nerves (X+XI). Another single foramen piercing the plate just medial to this fissure is an exit of the hypoglossal nerve. Extending ventrolaterally from the lateral part of the occipital condyle is a ridge (hereafter referred to as lateral ridge). The concave area delimited by the lateral ridge and the sphenoccipital torus receives the rectus capitis anterior, whereas the longissimus capitis must have inserted upon the sphenoccipital tubercle lateral to the last-named muscle, as judged from the muscle relations in *Ctenosaura* as described by OELRICH (1956). Above the lateral ridge the longissimus cervicis (denoted as the pars transversalis cervicis of the longissimus capitis by RUSSELL 1967) probably inserted, its supposed concave scar extending lateral to the semilunar nervous fissure upon the ventrolateral part of the paroccipital process (fig. 21).

The anterior surface of the proximal part of the exoccipital contributes to the internal ear cavity as illustrated by OELRICH (1956, fig. 12). As a rule, it produces a partial wall, between the lagenar recess and the occipital recess, made by a ventral process of the opisthotic. This process, called crista interfenestralis by OELRICH (1956) extends anterior of the tuberal crest between the foramen ovale and the entrance to the occipital recess and ventrally of the base of the sphenoccipital tubercle. GOW (1975) is correct in suggesting this process to be developed in all Sauria.

The paroccipital process articulates with the quadrate and both the supratemporal and the parietal or with the quadrate and the supratemporal only. It has two surfaces: the anterior and the posterior one, each of them differentiated into parts. The upper part of the posterior surface facing posterodorsally or dorsally is sometimes separated from the posterior one by a horizontal crest or bent. It probably received the ventral part of the rectus capitis posterior as it does in *Varanus* (see RUSSELL 1967). Based on the muscle reconstruction in *Platecarpus* made by RUSSELL (*l. c.*) the obliquus capitis was probably received by a posterior surface of the distal part of the paroccipital process.

The anterior surface of the paroccipital process (fig. 22) has an upper part overlapped by a posterior process of the prooticum and a lower one that contributes to the tympanic cavity. Two variants of the anterior wall of the paroccipital process that can be distinguished within the order Sauria differ by a disposition of their lower part, which can be directed ventrally or anteriorly. In the first case what is a true anterior surface is entirely covered by the prooticum, its apex, or the ventral part of its broadened posterior extremity being directed to the ventrodistal corner of the paroccipital process (fig. 22A, 20H, J). In the second case the prooticum overlaps merely the upper part of the anterior surface of the paroccipital process and its apex is directed towards the dorsodistal corner of this process (figs. 22B, 20A—G). The first type is characteristic of most Iguania and many Scincomorpha such as the Gerrhosauridae, Teiidae and the Upper Cretaceous groups, Macrocephalosauridae and Polyglyphamodonitdae as well as by two representatives of the anguimorphan group, the ones most loosely associated with the infraorder (*Paravanus* and *Bainguis*). It is suggested to be primitive for Sauria on the outgroup analysis (SCHAEFFER *et al.* 1972). The Anguimorpha tend to display the second type. *Varanus* and *Lanthanotus* are most typical in this regard, whereas the remaining genera are more or less advanced in the same direction. The second type, but clearly somewhat different variant, is developed by Gekkota such as Gekko and *Teratoscincus*. It is, by extension, regarded typical of this infraorder and is supposed to be achieved by parallel evolution.

Supraoccipital and metakinetic joint

The supraoccipital forms a dorsal rim of the foramen magnum and sutures with the exoccipital and prootics. It ascends anteriad to join the parietal by means of a cartilaginous processus ascendens or by a bony articulation. Its shape and the type of its contact with the parietal are the main features subject to variability. The slope of the supraoccipital is a function of both a horizontal distance between metakinetic joint and supraoccipitoparietal articulation, and the perpendicular distance between them, and thus of a length to height proportion of the posterior part of the dermatocranium, i. e. that which is directly subject to selectivity on biomechanical principles. Only the development of a long midline process of the supra-

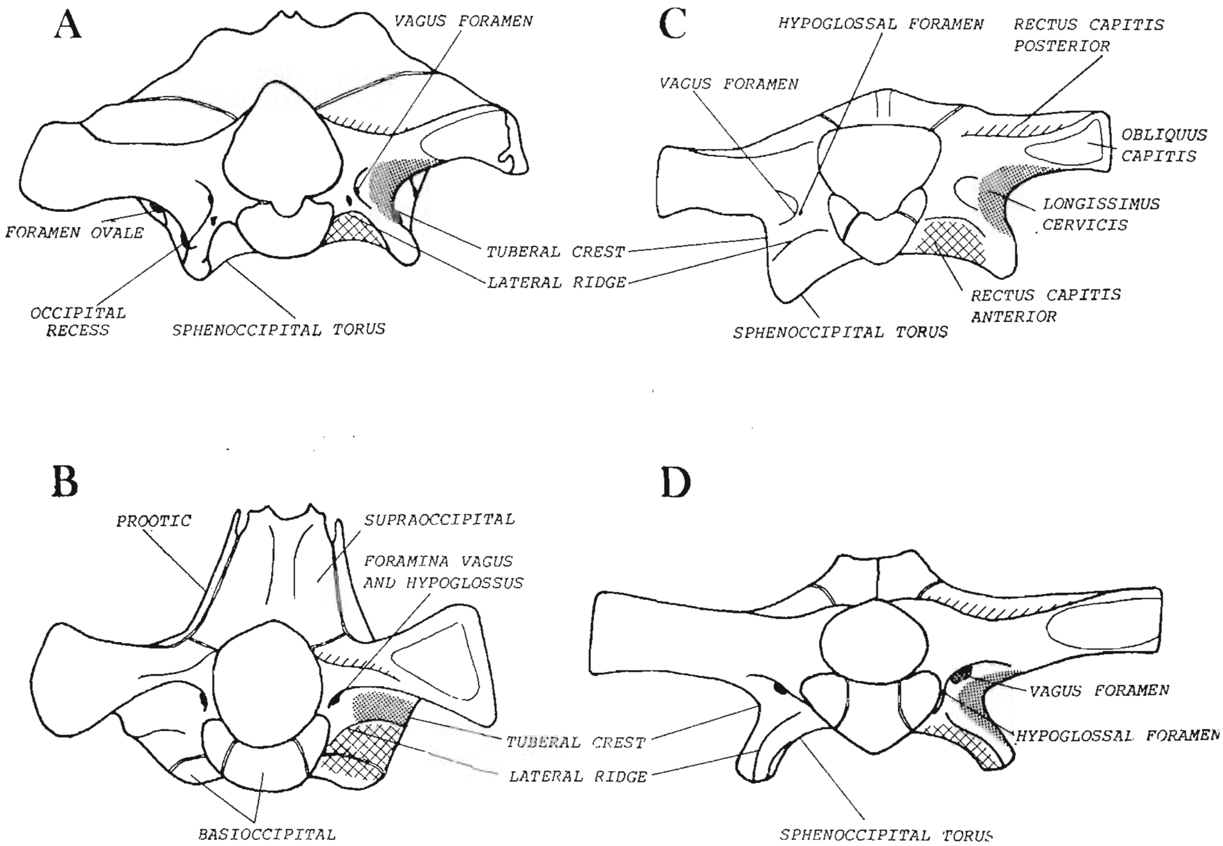


Fig. 21

Brain case structure in Sauria. Posterior view. A — *Xenosaurus grandis* MCZ 46785; B — *Varanus niloticus* HUB 95 (419); C — *Gobiderma pulchra* ZPAL MgR-III/64; D — *Telmasaurus grangeri* ZPAL MgR-I/65. Not to scale.

occipital (posterior to the pars ascendens tecti synotici) destined for making a joint with the parietal, which is found in many Scincomorpha but never in Anguimorpha, reduces the above correlation. Corresponding with a flat type of skull, a flat brain case with but slightly vaulted supraoccipital deprived of a high sagittal crest contacting with the parietal, is characteristic of all Diploglossa as well as of most Platynota, all the Late Cretaceous representatives of the present material included. It is also characteristic of the Late Jurassic *Dorsetisaurus purbeckensis* and is, thus, believed to be originally characteristic of the infraorder. Whether it is primitive (plesiomorphic) or shared derived of anguimorphan stems (synapomorphic) cannot be answered without greater knowledge of saurian ancestry. The earliest Sauria, the Permo-Triassic Paliguanidae, are similar to the Iguania in having a short and strongly ascending supraoccipital, judged on the overall appearance of their skull (see CARROLL 1975). Whether it is an ancestral group or sister group of autarchoglossan stem (including at least Scincomorpha and Anguimorpha) may not be decided for the time being.

The connection between the supraoccipital and the parietal is sometimes rather loose in Anguimorpha as e. g. in *Gerrhonotus*, *Ophisaurus*, *Abronia*, *Anguis*, and *Xenosaurus*, the gap being bridged over by the processus ascendens and by membranes. Such a state of this joint is correlated with a rather intensive metakinetic mobility, which is a component of the amphikinetic skull system of Sauria. The metakinetic mobility seems to be primitive in Sauria not only on what is known about the kinesis in vertebrates (VERSLUYS 1912, 1936) but also on the analysis of this joint within the suborder. Two types of the supraoccipitoparietal contact may be discerned within the infraorder Anguimorpha, differing, among others, by a method of insertion of the spinalis capitis. In the first one, occurring in the Diploglossa and the Lanthanotidae, the spinalis capitis inserts dorsally on the parietal, the scars forming a shallow step inclined but slightly downwards from the plane of the bone. Sloping still more posteroventrally, paired triangular processes of the posterior border of the parietal contribute to formation of the supraoccipitoparietal contact. They are usually situated on both sides of the processus ascendens. These processes partly cover the gap but do not join the supraoccipital in *Anguis*, while fitting closely to a straight anterior rim of the brain case in *Lanthanotus*, thus reducing mobility. Although closely related to *Lanthanotus* and similarly tending to the limitation of the metakinetic mobility, the Varanidae display a different type of the supraoccipitoparietal joint. Here, the spinalis capitis is received by a deep posterior border of the parietal extending downward and forward from the sharp posterior margin of this bone. The supraoccipital joins this border from below rather than from behind by means of an indented rim (*Varanus griseus*) or by paired processes suturing to the paired downward processes extending from the bases of the posterolateral extensions of the parietal (*Varanus niloticus*). The two types of supraoccipitoparietal joint exemplified by *Lanthanotus* and *Varanus* are two solutions to almost the same problem, not likely to be derived from one another but rather analogous and secondary. The most reasonable common ancestral state for them is one without processes bridging the supraoccipitoparietal gap (apart from the processus ascendens) but the dimensions of this gap are not known. Whether a supraoccipitoparietal contact like that of *Gerrhonotus* (see above) is primary in Anguimorpha or whether it is derived from an initial state with a narrower gap remains an open question but the first suggestion seems more convincing to me.

Brain case wall

The prootic (fig. 22) consists of two main parts. The lower part is a concave recessus vena jugularis which contributes to a tympanic cavity, the upper part consists of an inferior process, an alar process (sometimes absent) and a posterior process. Both parts taper posteriorly to produce a pyramid-like extremity overlapping the opisthotic and suturing to it. Separating these parts from each other, a prootic crest extends from beneath the inferior process upwards and backwards, towards the apex of the pyramid, constituting its edge. The recessus vena jugularis has the shape of an obtuse-angled triangle, crista prootica being its longest side (fig. 22A). Its posterior side is sutured to the opisthotic contributing to the foramen ovale. The anterior acute angle is directed to the entrace to the Vidian canal. Just superior to this part the subquadrangular inferior process extends anteroposteriorly to articulate with the parasphenoid+basisphenoid by its ventral side. Separating the inferior process from the alar process is a trigeminal notch. The alar process extends anterior to the anterior semicircular canal. The course of the anterior semicircular canal, which is posteriorly concave, is usually distinct at the surface of the prootic. Its upper part crosses the prooticosupraoccipital suture to extend within the supraoccipital where it is sometimes visible. The horizontal semicircular canal is hardly recognizable at the surface of the prootic but it must be looked for within a horizontal swelling extending from the center of the concavity of the anterior semicircular canal towards the posterior apex of the prootic. It curves medially before reaching this apex and enters the opisthoticum, but this part is deep under the bone surface. In fossil skulls the paroccipital processes are sometimes broken off external to this curve giving to the brain case artificial rounded outlines.

The course and form of the prootic crest are subject to variability. Its form changes from a low ridge to the extensive lamina of bone overhanging the recessus vena jugularis. The ridge or a base of the lamina may follow the course of the horizontal semicircular canal or may run a distance apart converging with it only posteriorly. The tympanic cavity being delimited by the prootic crest, its volume decreases when the crest goes down or it gets narrower when the

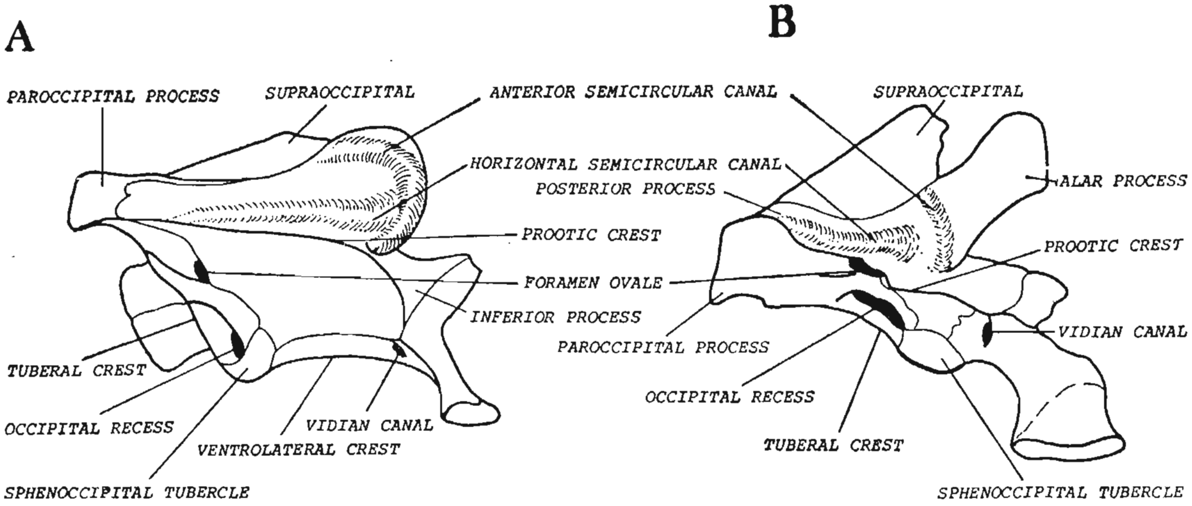


Fig. 22

Brain case structure in Sauria. Lateral view. A — primitive type based on *Paravaranus angustifrons* ZPAL MgR-I/67; B — Derived type based on *Varanus niloticus* HUB 95 (419). Not to scale.

crest gets a form of a lamina. The anterior part of the prootic crest provides an attachment for the aponeurosis of the origin of the protractor pterygoideus muscle and thus it certainly depends on the changing demands of this muscle. The variability connected with such local functional causes may, but does not absolutely need to interfere with the evolution of the brain case wall which is ruled by more general adaptive principles, such as e. g. the dependence of skull segment proportions on feeding biomechanics. The states of the prootic crest can hardly be classified as primitive or derived except for the course of its posterior part which is connected with a direction of the posterior process of the prootic. If it extends towards the ventrodistal corner of the paroccipital process, a state said to be primitive (p. 75) of Sauria, the posterior part of the recessus vena jugularis is subhorizontal and/or well exposed in ventral view which contributes to the primitive broad ventral aspect of the brain case (comp. figs. 4, 20, 22). The recessus vena jugularis extending vertically sometimes overhung by a long lamina of the prootic crest and the prootic crest directed to the dorsal corner of the distal extremity of the paroccipital process would be derived states of the characters of the brain case wall. The present material (*Paravaranus*, *Bainguis*) suggests that the primitive ventral aspect of the brain case is correlated with a lack of the alar process of the prootic. The examination of a comparative material partly endorses this statement. A broad recessus vena jugularis connected with a lack of the alar process is known in the Iguanidae (*Crotaphytus*, *Iguana*), the Agamidae (*Phrynocephalus*) and the Teiidae (*Ameiva*), the alar process being very small and superior to the anterior semicircular canal rather than anterior to it in other representatives of these families. The incipient alar process of the Macrocephalosauridae is associated with a very broad, ventrally exposed fossa vena jugularis and a triangular subhorizontal ventral surface of the paroccipital process. The same combination of character states was probably characteristic of *Prolacerta* and *Youngina* (Gow 1975). When considering the problem of the primitive versus derived character of the alar process, the great elasticity of this process should be kept in mind which implies that every type of alar process could have derived from any other type of this process. The alar process is produced by supplementary bone completing the brain case wall between the prootic and the parietal. Its shape and direction would depend on the same length to height proportions of the posterior skull segment as does the metakinetic joint (see p. 75) and is probably easy to be changed with changing skull proportions. In spite of this elasticity certain types of alar processes are characteristic of infraorders. The triangular alar process of Gekkota, with the alar crest passing onto the process protruding ventrolaterally which is uniquely derived for this infraorder, stands quite apart from the alar processes known in other infraorders. In Iguania the anterior semicircular canal always contributes an important part to the anterior margin of the brain case. If present, the alar process is a small sheet of bone extending over the posteriorly curving part of the anterior semicircular canal. Its upper margin (or, rather, apex) contacts the skull roof almost in the same transverse line with the metakinetic joint. Characteristic of Anguimorpha is a large alar process extending far anteriad of the anterior semicircular canal. It turns upwards only in the Varanidae. The anguimorphan type of alar process is paralleled by many Scincomorpha but this infraorder is much less consistent in this regard than are the Anguimorpha.

If we consider two distantly related lizards *Varanus griseus* and *Iguana iguana*, which have the same length to height proportions of the posterior skull segment and, consequently, exactly the same structure of the metakinetic joint and its surroundings, we can realize the differences in structure of the alar processes indicating their different origin. The alar process of *Varanus* is clearly derivable from the long anteriorly directed anguimorphan type by turning it upwards and the type of *Iguana* is not likely to be derivative of the same long type. This suggests that they are parallel structures. The most probable ancestral state for both of them is the one deprived of the alar process.

Conclusions

An extremely primitive condition of the brain case floor characterized by a parasphenoid reaching far posterior to overlap the basioccipital, is sometimes preserved at the preanguimorphan grade as exemplified by *Bainguis parvus* (fig. 20J). However, the shortening of the parasagittal part of the parasphenoid could occur very early in phylogeny, certainly prior to separation of Diploglossa and Platynota, for which the medially shortened parasphenoid connected with a trapezoidal sphenoccipital suture is a shared derived character state. A shortening of the parasphenoid is regarded as a parallel process in different infraorders of Sauria. The primitive brain case wall of Sauria is characterized by a low position of the posterior process of the prootic; a broad recessus vena jugularis; a ventral part of the anterior surface of the paroccipital process largely expanded in a subhorizontal plane and by a lack of the processus alaris of the prootic. Similar to the primitive brain case floor with a long parasphenoid, this type of structure of the brain case wall is supposed to be inherited from presaurian ancestors. Parallel in different infraorders, the evolutionary changes include a rotation of the posterior part of the recessus vena jugularis from a subhorizontal to a subvertical position and a development of a new part of the brain case wall anterior or anterodorsal to the anterior semicircular canal — the alar process.

The primitive structure of the brain case occurs at the preanguimorphan grade of the anguimorphan evolution (p. 67), while becoming modernized in both the Platynota and the Diploglossa. The structure of the brain case is much the same in both these superfamilies which suggests that it has been acquired in their common ancestor, or, at least, some of its character states have. Taking into account a certain variability of the brain case wall at the necrosaurian grade (p. 69) and in particular an intermediate character of both the ventral part of the paroccipital process and the recessus vena jugularis in *Gobiderma* as well as a probably underdeveloped alar process in Proplatynotia, the character complex directly ancestral to both superfamilies is proposed as follows.

Wheather plesiomorphic or apomorphic in Anguimorpha a very low, dorsally flattened brain case with quite a loose metakinetic joint and a trapezoidal sphenoccipital suture were characteristic of an ancestral form. I would suppose that the process of rotation of the posterior part of the recessus vena jugularis has only been initiated in this species to be continued in parallel in both groups of lizards. A fairly long anteriorly directed alar process was probably already developed at this evolutionary stage. It tends to become higher and shorter only in some lizards of the modern platynotan grade (Varanidae, Mosasaurinae). Derived in different anguimorphan stems and probably subject to parallelism is an increasing reduction of the metakinetic mobility which is probably connected with a simultaneous development of mesokinetic mobility and a modernization of hypokinetic mobility (see p. 86). A reduction of the posterolateral extensions of the parasphenoid brought about to the maximum in two modern platynotan lines, in *Lanthanotus* (but not in *Cherminotus*) and in *Varanus*, is connected with the anterior shift of the sphenoccipital tubercles caused by an anterior displacement of the rectus capitis anterior. It is supposed to be parallel in these lines.

Maxillary segment

Introductory comments

Although a detailed consideration of the function of the kinetic skull apparatus in lizards is out of the scope of the present paper, some observations concerning these phenomena are relevant in view of the obviously high degree of skull kinesis of the Late Cretaceous lizard fauna described herein. The examination of these skulls as compared to FRAZZETTA'S (1962) model of skull kinesis calls for some comments. Based mainly on this model many new data concerning the problem of cranial kinesis and other problems relevant to the latter have been published recently (RUSSELL 1964, JORDANSKY 1966, 1971*a*, 1971*b*, THROCKMORTON 1976, RIEPPEL 1978*a*, 1978*b*, SMITH 1980). My comments will concern:

— the influence of the occipital segment (a brain case) on the activity of the maxillary segment (a part surrounding the brain case and movably articulated with it, in terminology of *Versluys* 1912);

— consequences of the retraction on the floor of the skull apparatus of Sauria lacking a transverse rotary axis;

— the case of the interruption of the lower temporal arch and that of the loss of the vomeropterygoid contacts.

Recapitulation of main points of Frazzetta's (1962) model

The model consists of three skull segments movably articulated with each other and considered in projection on a sagittal plane. These are: (1) a triangular muzzle unit or snout, (2) a quadrangular posterior segment consisting of several units but constituting a functional entity and (3) an occipital unit or a brain case that is fitted into a posterior part of the posterior segment (2). The first two segments correspond to the maxillary segment of *Varsluys* (1912). The snout is considered a quite rigid part, triangular in projection. The posterior segment consists of four elements which are: a parietal or, more accurately, a constant distance between a mesokinetic and a quadratosupratemporal joint; the quadrates; the pterygoids and the constant distance between the mesokinetic joint and the posterior extremity of the maxilla. In projection each of these elements constitutes one link of a four link system characterized by constant (or almost so) side lengths and variable angles and referred to as a quadric-crank mechanism. The occipital segment is connected with the posterior segment by means of paroccipital processes in rotary joints (metakinetic axis), differing from the metakinetic joint, which occurs between the supraoccipital and the parietal. It is also connected with this segment by means of the basipterygoid processes in a sliding basipterygoid joint. A more loose connection occurs between the alar process and the parietal (not considered in the model). In such a skull mechanism protraction and retraction of the snout result from the movements of the

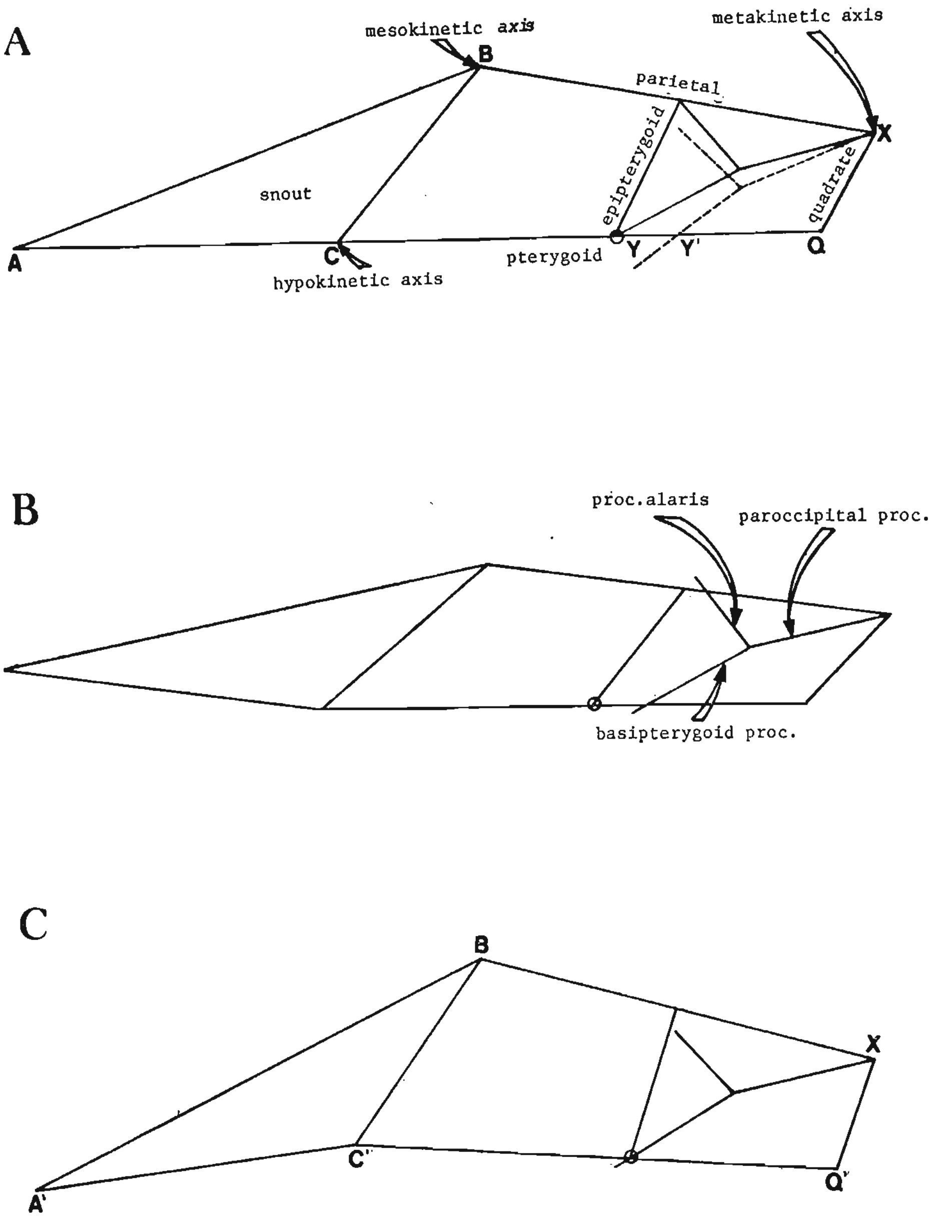


Fig. 23

Frazzetta's (1962) model of skull kinesis in lizards slightly emended by considering the mobility of the occipital segment. A. Resting phase of the cranial lineage mechanism. Solid line — relation between the occipital segment and the maxillary segment, assuming the lack of metakinetic mobility. Dashed line — Position of the occipital segment allowing retraction in the case of preservation of metakinetic mobility (according to Frazzetta the parietal is uplifted relative to the occipital unit during the retraction). B. Protraction in amphikinetic skull; C. Overretraction in amphikinetic skull. Notations ACQ and A'C'Q' correspond to those in figs. 24 and 25.

posterior skull segment generated by muscles acting on the pterygoid and on the quadrate (by means of a quadratomandibular joint) respectively. The retraction of the apparatus leads to a lowering of the snout below its resting horizontal position (see fig. 23C). I would propose to call it an overretracted position as differing from a retracted position of the nonsquamatan diapsids which was, at least primarily, identical with a resting one (fig. 23A). According to Iordansky (1966) the overretracted position, characterized by a concave palate, has evolved in lizards as an adaptation for better holding of the prey (for other hypotheses see Frazzetta

1962 and IORDANSKY 1966), a purpose for which a retractory function has been more important that the protractory one. IORDANSKY'S view that this position has been of importance for predators living on rather small preys but not much smaller than the predator's mouth, seems reasonable. This type of predatory habit would be thus characteristic of lizard ancestors, and the possibility of overretraction would be the main subject acted upon by selection. I suggest that this particular character, being the main distinction between the squamatan and the nonsquamatan diapsid evolution, has caused other differences between these two groups at least in what concerns metakinetic mobility and the structure of skull floor.

Influence of the occipital segment on the activity of the maxillary segment

I believe that VERSLUYS (1936) was correct in regarding the internal knob-like processes of pterygoids as a sort of brake for these bones. In the primitive diapsids these processes made up an anterior and ventral limitation of the basipterygoid joint, preventing both further retraction of the pterygoids and disarticulation of the joint. As was clear to FRAZZETTA (1962), experimentally forced movements of the maxillary segment produce corresponding movements of the occipital segment, the basipterygoid processes being protracted by protraction of the snout and retracted by its retraction. This is supported by my own observations on specimens of partly dissected skulls of *Xenosaurus* and *Lacerta* immersed in hot water and operated by hand. However, in living animals the maxillary segment cannot evoke any movements of the occipital segment, that provides its only support. One should rather assume that the maxillary segment changes its position with respect to the occipital segment (assuming the latter to be fixed), while changing its shape. The retraction of the pterygoid should, thus, be considered in relation to the parietal unit rather than to the basipterygoid process, the amount of shift in the basipterygoid joint being the resultant of very complex movements.

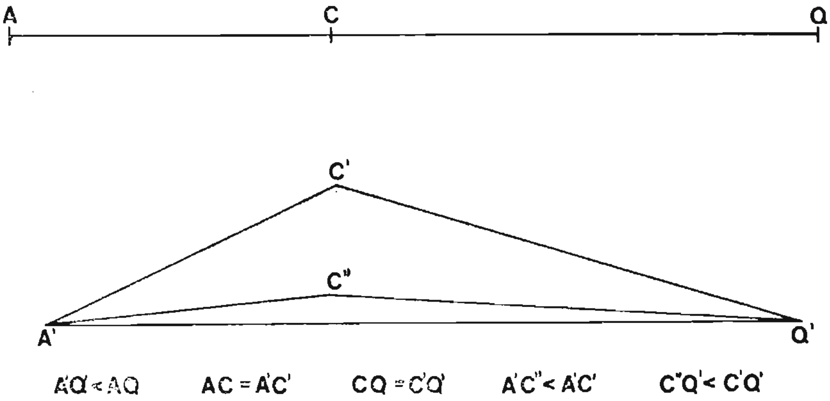


Fig. 24

Diagram of the skull floor (AQ) showing the effect of the overretraction on this part of the four-link system of lizard skull of FRAZZETTA (1962) when the hypokinetic axis C′ is either developed — position A′C′Q′ or not — position A′C′′Q′

A comparison of the effects of retractory movements on the basipterygoid region of the amphikinetic skull and that of the monomesokinetic skull (see fig. 23A) sheds light on the significance of the preservation of metakinetic mobility in Sauria.

As stated by FRAZZETTA (1962) the parietal is uplifted relative to the brain case at the metakinetic joint in the retractory phase of the amphikinetic skull. This is impossible in the case of the monomesokinetic skull. The upward movement of the parietal must absolutely be associated with the rotation of the whole maxillary segment clock-wise relative to the brain case (as shown in fig. 23A) and, consequently, in the moving apart of the basipterygoid process and the pterygoid part of the basipterygoid articulation to produce a gap between them (distance Y—Y' in fig. 23A). Given that the internal processes of the pterygoids serve as a brake on retractive movements of the pterygoids, the appearance of this gap would permit to retract the pterygoids beyond the resting position (fig. 23C). As stated by FRAZZETTA (1962) the adaptive implications of the double kinetic condition were not obvious to him. I suggest that the preservation of metakinesis in the squamatan line was necessary for overretraction of the cranial linkage mechanism, a difference from some other diapsids, in which the resting position is still the limit of retraction and the metakinetic mobility is lost.

The assumption of the blocking function of the basipterygoid joint in overretraction implies that the overretracted position could be attained by a skull having lost its metakinetic mobility by reducing basipterygoid processes or by diminishing pterygoid bending and by reducing its internal knob-like processes. The first solution is used in neognathic birds, which achieved an overretracted position of a sort (IUDIN 1970), the second one in modern, mesokinetic lizards such as *Anniella pulchra* and *Lanthanotus borneensis.* These cases substantiate a supposition that the fully developed basipterygoid articulation would prevent overretraction if the brain case was immovably fused to the parietals, and support the hypothesis about the importance of the preserved metakinesis to the development of overretraction in Sauria.

Influence of retraction on the skull floor of Sauria having no hypokinetic axis

FRAZZETTA'S model based on *Varanus* has its basal unit, i. e. a pterygoid, connected with muzzle unit or snout by a hinge joint, a type of transverse rotary axis. Such an axis, which will be referred to as hypokinetic axis (after RUSSELL 1964), is absent from many lizard groups such as most of Iguania, the Lacertidae and Diploglossa. FRAZZETTA who knew this deficiency has neglected it. He assumed a certain flexibility of the palate to compensate for the lack of the hypokinetic axis in these lizards, in which he was probably correct. Two types of palate structure have been recognized by IORDANSKY (1966) among the extant lizards he studied. Type I characterized by a non-subdivided pterygopalatine bar and an oblique immovable pterygopalatine joint was recognized in *Cyclura, Agama* (both Iguania) and in *Ophisaurus* (Anguimorpha). The hypokinetic type called type II by IORDANSKY occurs in varanids, geckos as well as in different representatives of Scincomorpha. The palate of the Late Cretaceous Anguimorpha, *Parviderma inexacta, Saniwides mongoliensis* and *Telmasaurus grangeri* described herein, recalls IORDANSKY'S type I but is presumed to have displayed the mobility of pterygopalatine joint in a horizontal plane, the pterygoids having probably slided over the oblique and even surfaces of the palatines (see fig. 10). Such a mobility of this joint cannot be directly proved on the fossil material, but, if it is assumed, it contributes, along with a reduction of the vomeropterygoid contact and of the quadratojugal, to a hypothesis of the development of the skull kinetic mechanism in saurian phylogeny.

The lack of the hypokinetic axis is obviously primitive in Sauria. FRAZZETTA'S model, which is a fairly good approximation of the skull of *Varanus*, is much less similar to the case

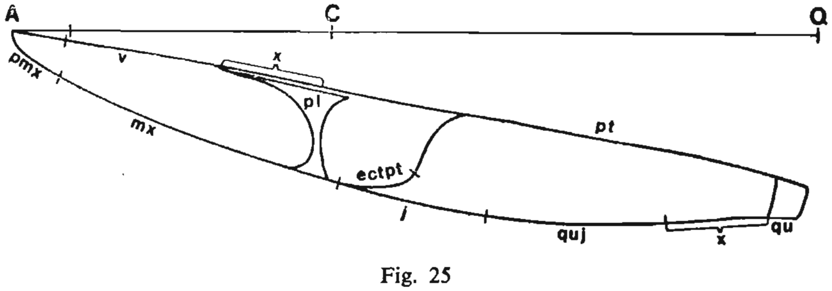


Fig. 25
Diagram of the skull floor, in ventral view, with regions of possible shortening indicated by x. For abbreviations see p. 10.

of the primitive skull. The primitive skull may, rather, be regarded as an inflexible beam (because of the rigidity of the skull floor) that is forced to bend into a ventrally concave curve. I would presume the existence of the contracting stresses within the skull floor, acting from its ends towards the middle, during this bending. The methods of setting the skull mechanism to an overretractive position (by retraction of the quadrate) suggests the existence of stretching forces rather than the contracting stresses. However, it should be kept in mind that the final effect of overretracting (no matter how it is achieved) is the ventral bending of the beam (skull) and thus bringing closer its ends as demonstrated in fig. 24 (AQ A'Q'). The bones constituting the skull floor would retain their lengths only if they were bent at a particular angle relative to one another because their lengths and the distance between the skull ends determine a triangle. If, because of rigidity of the skull, the bones of the skull floor were not able to bend, they would be subject to shortening (see figs. 24, 25). A reduction of both pterygoid and quadratojugal along with formation of the sliding pterygopalatine joint, constitute a complex of changes consistent with the presented model (fig. 25) of reducing of the horizontal stress on the skull floor. However, the actual sequence of these changes in saurian phylogeny is not directly implied by the model.

Evolutionary changes of the palate of Sauria

The palate structure of the Late Cretaceous Central Asian Platynota suggests that horizontal stress, acting on the skull floor by overretraction, has been reduced by a simple shortening of the anterior extremity of the pterygoid, its shortened, strongly tapering palatine process having slid over the medial shelf of the palatine (see e. g. pl. 13 : 2a, figs. 10B, 14B). In juvenile stages of recent lizards (Iguania, Teiidae, Lacertidae, Cordylidae and Anguidae), LAKJER (1926) has shown the presence of an isolated anterior part of the pterygoid, a so-called hemipterygoid, eventually fusing with the palatine. As shown by this author, the hemipterygoid has an overlapping suture with both the vomer and the pterygoid, which permits for a certain amount of sliding movement i. e. a certain amount of shortening of the palate. This could represent a first step on the way to the interruption of the medial strut of the skull floor, probably characteristic of primitive lizards and inherited from them by some lizard groups at least.

Although he has not given any evidence for the presence of the hemipterygoid in *Varanus*, *Heloderma* and in geckos, a lack of evidence does not conclusively point to the absence of the bone. I would suggest that it either disappeared or fused very early with the palatine in highly kinetic lizards. In the second case, it would correspond to the medial shelf of the palatine, which is beveled from the plane of the palate and overlapped by the anterior process of the pterygoid. Whether lost or fused, this bone disappeared very early from between the vomer and the pterygoid making thus a space for their being pushed together in the overretractory phase. In contrast, the hemipterygoid bridges the gap in the Iguania, Teiidae, Lacertidae, Cordylidae and Anguidae (Type I of IORDANSKY 1966). Although the type of the platynotans may be regarded as a more derived state of palate structure, with regard to efficiency of the overretractory movement, it seems not likely to be phylogenetically derivable from the type I, but could have derived independently from the type having a preserved pterygopalatine contact, instead.

Characteristic of the Platynota is a tendency to a shortening of the main body of the palate (fig. 26). Resulting from this tendency the palatine of the Platynota is readily distinguishable from that of other groups of lizards. Its maxillary process has a slender stalk differentiated from the shortened and narrowed main body and directed almost transversally. This palatine shape is correlated with a retraction of the internal nares, which tends to suggest its being a result of this retraction and, indirectly, of the retraction of the external nares characteristic of the Platanota. However, the examination of the present material and particularly of the lizards

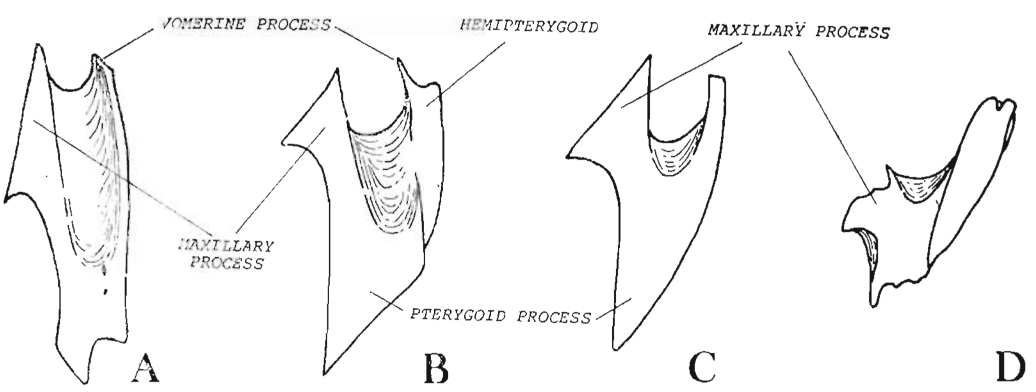


Fig. 26
Types of palatal structures in Sauria. A — *Tupinambis* sp. HUB 1050/35. 588, B — *Gerrhonotus* sp. ZPAL R-I/15, C — *Xenosaurus grandis* MCZ 46785, D — *Varanus niloticus* HUB 95 (419), A, B — Primitive saurian structure; C, D — Two derived states of Anguimorpha. Not to scale.

of the necrosaurian grade (see p. 25), indicates that the retraction of the choanae (i. e. a shortening of the palatine) was antecedent to the retraction of the external nares and not likely to have been caused by the last named process. Although a rôle of the palatine by the action of the kinetic skull apparatus is far from being understood, I believe that its spool-like shape with transversally directed axis has much to do with the skull kinesis. It could be hypothesized that its movement in the cranial linkage mechanism could be a reason for the retraction of the choanae and indirectly of that of the external nares. The hypothesis should, however, be verified by subsequent studies.

Loss of quadratojugal

Several hypotheses concerning the problem of the interruption of the lower temporal bar were put forward by Versluys (1912), Lakjer (1926), Iordansky (1966), Robinson (1967) and others, most of them recapitulated by Iordansky (1971). Most of these ideas associate the loss of the quadratojugal with two factors: 1) kinetic movements of the skull along with streptostyly of the quadrate and 2) the loss of biomechanical importance of the lower temporal arch (Carroll 1977). According to the model presented in fig. 25, the forced bending of the primitive diapsid skull of saurian ancestor caused longitudinal contracting stresses within the skull floor which was loosened by the reduction of both its medial and lateral struts. The model implies that both these reductions contributed to the development of overretraction but it does not absolutely indicate their being synchronous. Recent literature affords many examples of the nonsquamatan diapsids having an incomplete lower temporal bar along with a preserved vomeropterygoid contact. These are *Prolacerta* (Gow 1975), *Tanystropheus* (Wild 1973, 1980), *Macrocnemus* (Kuhn-Schnyder 1962), *Glevosaurus* (Robinson 1973) and *Gephyrosaurus* (Evens 1980) as well as *Kühneosaurus* considered as saurian representative by Robinson (1972) but included into the range of Eosuchia by Evens (1980). According to Evens all these reptiles possessed fixed quadrates and, consequently, akinetic skulls. This suggests that: 1) the interruption of the lower temporal bar was the first "saurian" character to appear in the diapsid evolution and 2) that it was caused by some factors independent of the streptostyly — the point of view advocated by many recent authors (Carroll 1977, and Iordansky 1971 among others). It will be, thus, concluded that the interruption of the lower temporal bar was a preadaptation from the point of view of the development of the overretraction of the cranial mechanism in Sauria.

Conclusions

The interruption of the lower temporal bar probably occurred before the differentiation of the saurian stem from the diapsid reptiles whereas the streptostyly appeared in direct saurian ancestors and was probably independent of the streptostyly occurring in archosaurs. Typical of the saurian stem was a tendency to depressing the snout unit of the cranial linkage mechanism below the resting position — the attitude having positive selective value in Sauria. It has been shown (fig. 23 A) that the flexible connection between the brain case and the maxillary segment (metakinetic mobility) allow an increased retraction of the skull linkage mechanism. It was presumably necessary for overretraction of the mechanism, assuming that the basipterygoid joint has been anteriorly checked. At the initial phylogenetical stage of overretraction, the flexibility of the dorsoventrally flattened palate bones was probably sufficient to permit a certain ventral bending of the snout. At this stage, the maxilla, which was a lateral dorsoventrally extended element of the snout having no ability of ventral bending, must have been shifted a little bit backwards, the development of a sliding maxillopalatine joint being of importance to this shift. It was facilitated by the anticipatory reduction of the quadratojugal. A further development of overretraction resulted in breaking the rigid vomeropterygoid contact. This probably occurred by a progressive reduction within a slender tapering anterior process of the pterygoid and has resulted in a separation of this process as an individual bone unit (a hemipterygoid) movably articulated with both the pterygoid and the vomer but eventually fusing with the palatines. It seems possible that the intensity of these changes has been subject to variability. They have probably been much accelerated in advanced predators in which the important rôle of overretraction has resulted in an increased horizontal stress on the skull floor. In these lizards the anterior part of the pterygoid has probably been lost. Formation of a sliding pterygopalatine joint has brought about intensification of the abduction of the lateral parts of the snout unit.

A universal value of the transverse disposition of the pterygopalatine joint for a kinetic skull apparatus (of any intensity of movement) has caused an independent and similar displacement of this suture in different lizard groups. This however, has not concerned the lizard groups of a conservative kinetic type, such as the Diploglossa and Iguania (IORDANSKY'S 1966 type I).

A possibility of contraction of the skull floor having been achieved, selection intensity on the increased flexibility of the palate was probably much decreased. In the lizards of IORDANSKY'S type I, a tendency to a strengthening of the skull floor probably made for a secondary immobilization of the pterygopalatine joint or they have quite omitted the mobile stage of this joint. Some of them have developed only a slight flexibility of the palate bones, sometimes having used additional clearances of the skull floor, as e. g. that of the pterygoquadrate joint (the case of *Lacerta* — after IORDANSKY 1966). Some others (Agamidae) have become stiffened in the overretracted position of the palate which thus became their resting position, skull kinesis having lost its adaptive value in this way.

The development of different specializations, such as a hypokinetic pterygopalatine joint, straightening of pterygoids or reduction of basipterygoid processes, allowing an undisturbed ventral bending of the maxillary segment in overretraction, reduced the importance of the metakinetic mobility which tends to disappear in specialized lizards (*Varanus*, *Anniella*, *Lanthanotus*).

Osteodermal skull covering

Introductory comments

Two main types of the osteodermal covering of the skull roof are present in Anguimorpha. The first one is a large-plate or shield pattern known from all the extant Anguidae, Late

Cretaceous *Odaxosaurus piger* and the *Melanosaurini* SULLIVAN, 1979. It is also represented in Late Cretaceous *Bainguis parvus* described in this paper. This type is characterized by a large, usually paired frontal scute and paired frontoparietal scutes tending to invade laterally the frontoparietal suture, as well as by a paired set of supraorbital scutes. Allowing for a certain variability in proportions of the scutes, this pattern is exactly like that displayed by Scincomorpha (the Gerrhosauridae, the Cordylidae and the Lacertidae). The second type which may be called a small polygonal plate pattern or small-plate pattern occurs in the Late Cretaceous species *Proplatynotia longirostrata*, *Gobiderma pulchra* and *Parviderma inexacta*, as well as in the Helodermatidae and the Glyptosaurini. It is also represented but in reduced and modified form, in the Varanidae.

Historical comments

The osteodermal covering of lizards has many times been discussed within a systematic context beginning with MARSH (1871). CAMP (1923) reviewed the extensive studies of OTTO (1909), STEHLIN (1910) and SCHMIDT (1910—1915) concerning the embryological development of the osteoscutes, their relation to epidermal scales, their variability, both within the range of the suborder and over different parts of the body as well as their phylogeny. Summing up the controversial opinions of these authors as well as his own observations, CAMP (1923) stated that the uniform squamation on all parts of the body and osteoderms composed of many small diffuse granules contributed to the primitive dermal covering of lizards. The diversification of the dermal covering of the skull in the lizard phylogeny appeared as an independent problem with the first description of *Glyptosaurus* by MARSH (1871). The inclusion of *Glyptosaurus* into the family Anguidae, first done by ZITTEL (1890), then discussed and accepted by GILMORE (1928) and substantiated by more recent and extensive data in MESZOELY (1970), caused a direct confrontation of two basic types of the skull dermal covering, a shield pattern versus small polygonal plate pattern. MESZOELY *et al.* (1978) regarded a shield pattern as primitive for the family Anguidae but they did not discuss the antiquity of this character state. SULLIVAN (1979) was more explicit about this problem. He believed that the shield pattern of the osteodermal skull covering of the Anguidae is homologous rather than parallel to the similar skull covering of Scincomorpha.

Initial stage of the dermal skull covering autarchoglossan stem

The above opinions of SULLIVAN (1979) include some very important implications. If the osteodermal skull coverings of both Scincomorpha and the Anguidae are really homologous, their pattern should have existed in a common ancestor of both Anguimorpha and Scincomorpha. Such a common ancestor must have antedated the Late Jurassic, when both groups first appeared. The transition from a uniform granular scale pattern, said to be primitive of all Sauria, to the shield pattern must have taken place then. Although I cannot fully agree with SULLIVAN'S concept of evolution of the osteodermal skull covering in lizards (see above), the supposition that the separation of the autarchoglossan branch from the main lizard stem included a formation of a new type of the dermal skull covering seems reasonable. But I would suggest that this divergence affected the epidermal covering rather than osteodermal ossifications of the dermis, which were probably at the initial stage of development. A large-element epidermal skull covering and irregular, strongly variable osteodermal incrustations are, thus, assumed to have contributed to the initial dermal skull covering of Autarchoglossa. This type of epidermal covering is assumed to be a character state shared by anguimorphan superfamilies.

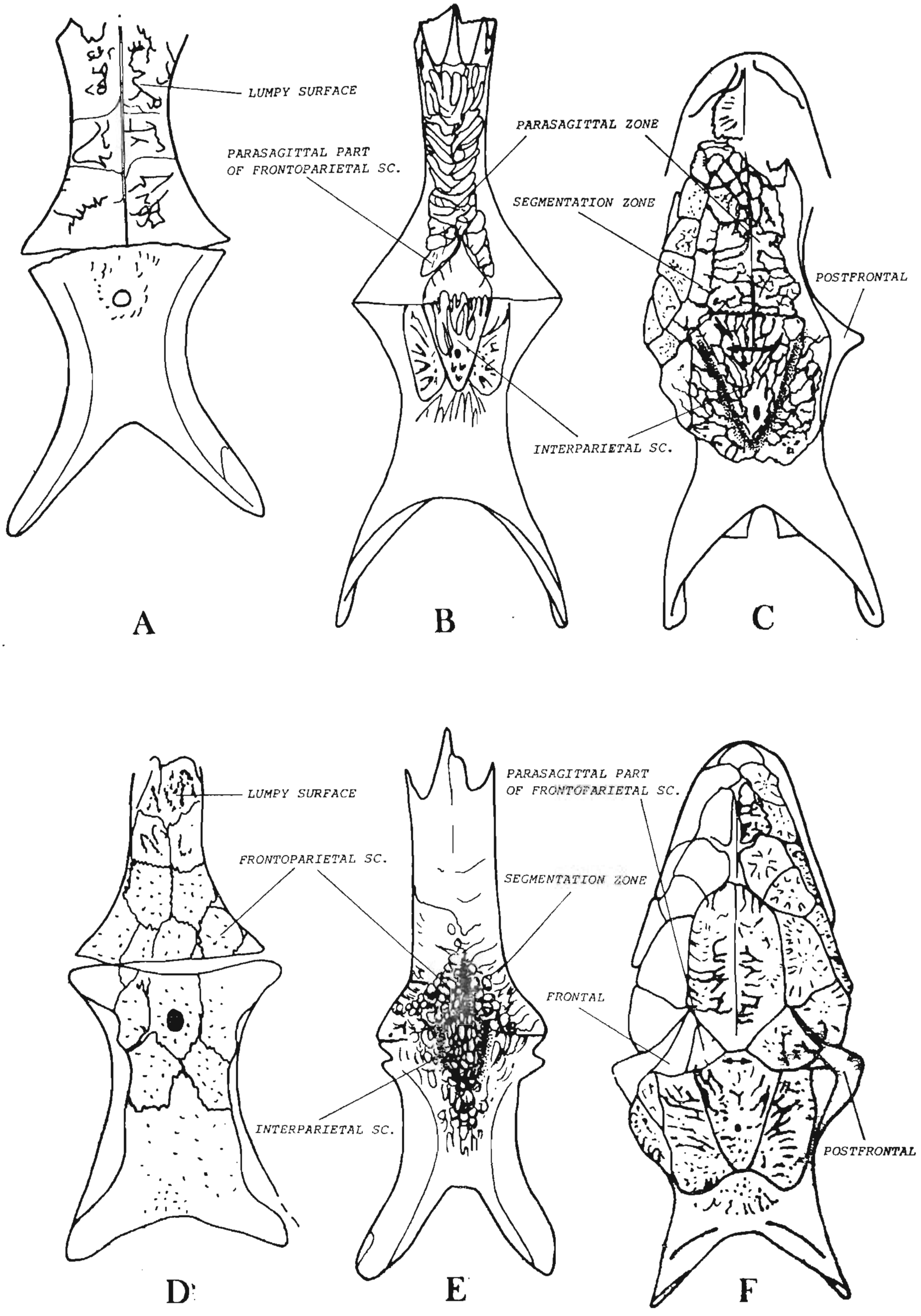
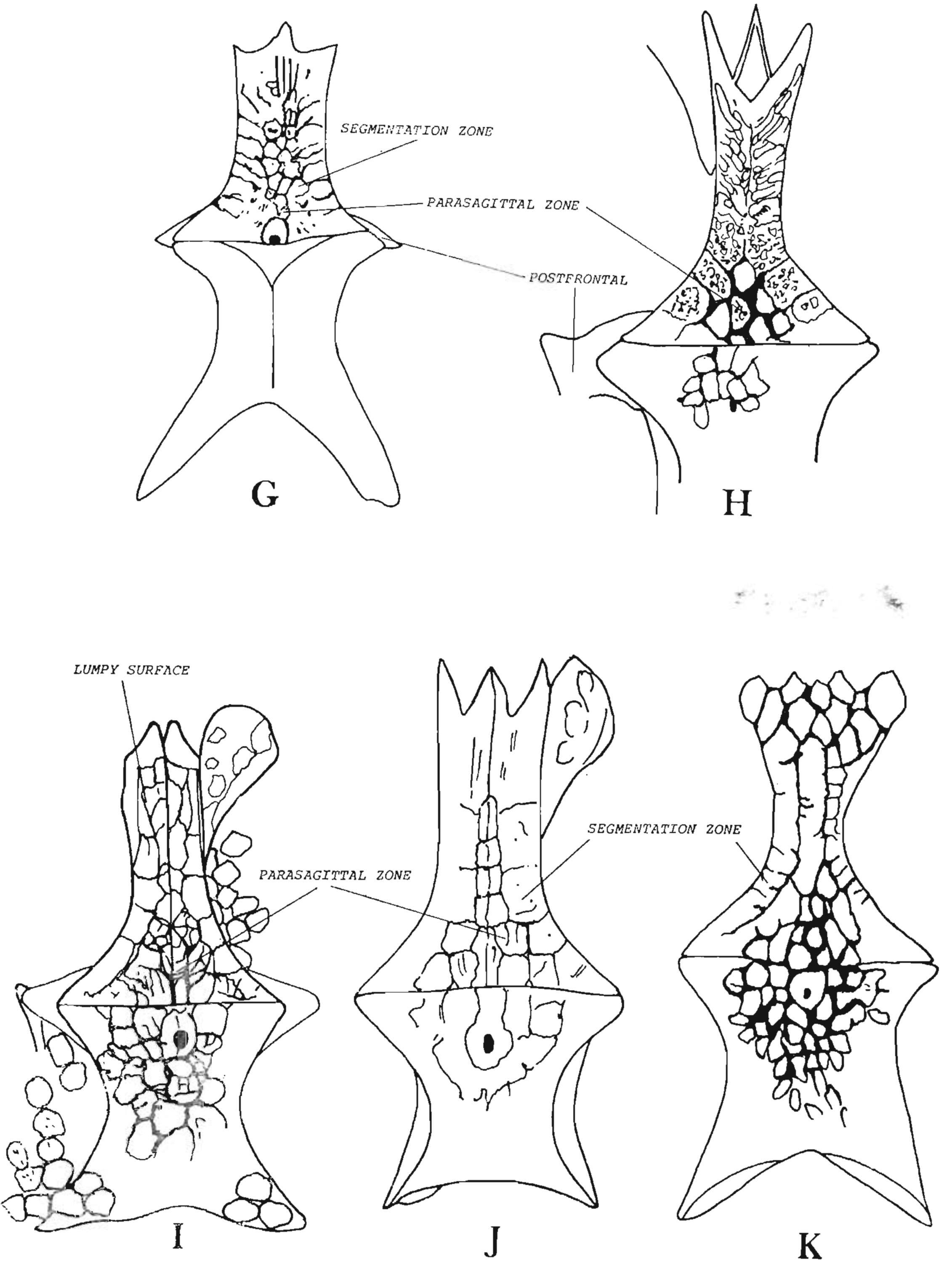


Fig. 27

Osteodermal skull covering in Sauria. Shield pattern (A—F), small-plate pattern (G—K). Note the differences (eventual pattern of parasagittal zone) and similarities (presence of segmentation zones, uniformity of incrusting elements). A — *Dorsetisaurus purbeckensis*, reconstructed from two specimens (after HOFFSTETTER 1967: figs 11B, the frontal and 11C, the parietal); B — *Gerrhonotus leiocephalus* ZPAL z. p. R-I/12, juvenile; C — *Anguis fragilis* ZPAL z. p. R-I/5 young adult;



D — *Parasaniwa wyomingensis*, reconstructed from two specimens by ESTES (1964, fig. 63); E — *Tupinambis* sp. HUB 1050/355888 adult; F — *Ophisaurus apodus* ZIN unnumbered specimen; young adult; G — *Ctenosaura* sp. ZPAL z. p. R-I/8 adult; H — *Parviderma inexacta* MgR-I/43; I — *Gobiderma pulchra* ZPAL MgR-III/66; J — *Proplatynotia longirostrata* ZPAL MgR-I/68; X — *Xenosaurus grandis* MCZ 46785 adult. Not to scale.

Relations between the epidermal and true dermal skull coverings

The known mutual dependence of the mesodermal and epidermal components of the dermal armour (see e. g. SCHAEFFER 1977) is taken as a basis for the assumed relations. I would hypothesize that the type of epidermal skull covering depends on the underlying skull roof bones, the closer the contact of the bones and the epidermis the stronger the dependence. This is supported by the fact that the large scale covering develops only in the regions of the intimate skin adhesion to the bones and precisely over the parasagittal part of the skull roof. The development of the osteodermal skull covering, which is successive to the skull bone and scale formation in the ontogeny is probably induced by a scale covering, the osteodermal units tending to eventually fit the scales. The lack of correspondence in extent between the osteoscutes and the horny scales in the adults of certain lizard groups (e. g. in the Scincidae) as well as composite nature of the osteoderms in certain lizards (mosaic pattern of the Scincidae, fusion of osteoderms covered by several scales or a doubled nature of the osteoscutes covered by a single scale in the Anguidae, fig. 27F) are probably caused by mechanical strength adaptation or by a specific type of growth and do not contradict the general rule.

Ontogenetic development of the osteodermal skull covering

The parasagittal zone of the skull roof (fig. 27B) is first subject to the osteodermal incrustation by apposition of the bone tissue. It contrast, in more lateral parts of the skull roof the bone tissue is deposited within the dermis and may, but does not always fuse with the underlying bones. The lateral corners of the parietals and the frontals, which are very often slightly curved ventrad as well as the posterior part of the parietals where the neck musculature causes a certain uprising of the skin, remain naked in the young osteogenetic stages, becoming covered by loose osteoderms only later in ontogeny (fig. 27B, C, F). A subdivision of the frontoparietal osteoscute covered by a single scale in the Anguidae (e. g. *Ophisaurus*, fig. 27F) results from the fact that its medial part belongs to the parasagittal zone of the close adhesion of the skin, whereas the lateral one develops in the skin, away from the skull bones. Outside the zones of intimate adhesion of the skin the shape of osteoscutes and that of scales are determined by skin properties, formation of small polygonal elements being a common method of covering of large surfaces known all over the living world, based on simple mechanical rules and easily recurrent. In the lateral parts of the frontal scutes, which are in the shape of long and narrow stripes (fig. 27, segmentation zones) this tendency to multiplication of the lateral armour turns into one to segmentation, which is usually manifested in the sculpture of the orbital borders of the frontal (fig. 27C, E, G—K). Here, this tendency is mainly the result of the influence of the nearby skin covering the orbits. I would suppose that the breadth of the frontals and their transverse profile have much bearing on the relative breadths of the segmentation zone, and parasagittal zone, and indirectly on the osteodermal covering pattern. Large flat frontals probably favour a broadening of the parasagittal zone at the expense of the segmentation zone and conversely. As suggested by figs. 27G—K, the closing together of the segmentation zones resulting in a drastic narrowing of the parasagittal zone involves a distintegration of the osteodermal covering of the latter because large elements can no longer fit into the narrowed central part of the frontals. The reason for such a medial shifting of the segmentation zones can be a strong narrowing of the frontals which is very often associated with their sinking in between the protruding orbital borders. However, a comparison of the frontal proportions and skull covering pattern in *Gerrhonotus leiocephalus* (fig. 27B) and in *Parviderma inexacta* (fig. 27H), the proportions of which are very similar in spite of a different osteodermal covering pattern, suggests that other factors may intervene.

The small-element osteodermal covering seems to be more favourable to mesokinetic mobility than is the osteodermal covering of the shield pattern, the mesokinetic joint being invaded either by the interparietal scute (anguid type) or by the frontoparietal scutes (lacertid type) in the case of the shield pattern.

A drastic increase of absolute body size could be, in my opinion, a third stimulus to disintegration of the osteodermal skull covering. Connected with this, a thickening of the dermis may probably cause a decrease of adhesion of the epidermis to the skull bones and reduces the influence of the skull roof bones on the squamation pattern and, indirectly, on the developing osteodermal covering. This is probably the case of the Glyptosaurini and the Platynota. This tendency has resulted in a complete loosening of contact between the osteodermal covering and skull bones in advanced, large-sized representatives of the Platynota, with *Gobiderma*, the Helodermatidae and the Varanidae being morphological grades of this process. It has probably been associated with a tendency to reduction of the osteodermal covering in the advanced Platynota, connected with the highly predaceous character of the group.

I would suppose that, once stabilized, the osteodermal skull covering had a certain tendency to conserve its pattern in spite of influences tending to change it. This is probably the case in some large-sized Scincomorpha that still display a shield pattern of the osteodermal skull covering, as well as that of *Gerrhonotus* having rather narrow frontals but still conserving a large-plate pattern. The latter (fig. 27B) seems to have come to the end with its large plate which would probably be broken into small elements if constriction of the frontals progressed. In such instances, the influence of more than one factor at a time would more securely cause a change of skull covering pattern than the influence of only one. As mentioned above, the development of the osteodermal skull covering begins with incrustation of the parasagittal zone with the irregular bone thickenings of different shape, variating from tubercles to ridges, separated by irregular furrows containing blood vessels. This early ontogenetic stage of osteodermal incrustation is to be seen in young skulls of some Anguidae (see e. g. *Gerrhonotus leiocephalus*, fig. 27B) as well as on the peripheral (e. g. less incrusted) parts of frontals of *Gobiderma* (fig. 27J), *Parviderma* (fig. 27H) and *Proplatynotia* (fig. 27K) and the Iguanidae (fig. 27G). It also occurs in different lizards of both autarchoglossan and nonautarchoglossan stems characterized by only rudimentary sculpture such as the Teiidae (fig. 27E) and the Iguanidae and in the earliest late Jurassic representatives of both Scincomorpha and Anguimorpha as illustrated by HOFFSTETTER (1966). The pit and ridge sculpture occurs on the maxillae of *Saurillus obtusus* and *Paramacellodus oweni* (Scincomorpha) whereas the frontals, known in *Saurillus obtusus* only, bear a sculpture of isolated tubercular bone thickenings. This type of osteodermal covering, if more densely deposited, produces a continuous layer of bone with an irregular sculpture consisting of ridges, furrows and pits, sometimes having a lumpy aspect (fig. 27A, D, I anterior parts of frontals).

Regarded primitive on both commonality and ontogenetic principles, the described type of the osteodermal skull incrustation may have readily changed into both small polygonal plate type and a shield type by simple growth. Which type would eventually evolve, obviously depends on the pattern of the epidermal scaling. The method of growth of the armour from irregular small units make this dependence nonexistant in early ontogenetic and phylogenetic stages. According to my view the most common type of growth of the osteodermal covering in lizards is by apposition of new bone tissue over the surface of the skull bones or that of previously formed osteodermal bone thickening, so as to turn the furrows containing vessels into the canals. Although this type of growth differs from a typical circumferential growth, it still causes a certain circumferential extension of small elements. A small plate pattern, or tesselated pattern, occurs when the small uniform epidermal scales induce a uniform disposition of ossification centres which increase to eventually touch themselves. Sometimes, but rather exceptionally, this may be succeeded by a fusion of small elements into a continuous layer (as, e. g., in some specimens of *Gobiderma pulchra* from the present collection (pl. 6 : 1, 4) but a tesselated pattern is not any usual stage of armour ontogeny antecedent to the shield pattern stage.

Conclusions

A large-scale pattern of the epidermal skull covering which has been assumed (see p. 87) for the common ancestor of the autarchoglossan lizard groups is not presumed here to be associated with a shield type of osteodermal covering. The ancestral osteodermal pattern was probably an incrustation of irregular bone thickenings separated by furrows containing blood vessels which turned into canals with a progressing deposition of the bone tissue. I would suggest that this type of osteodermal skull covering did not evolve into a more specific type before the appearance of the independent scincomorphan and anguimorphan lines and it was probably subject to important variability at this time. As regards further diversification of the osteodermal skull armour in phylogeny, we may consider two alternative hypotheses (fig. 28 A, B). Either the shield type (fig. 28 A, 2′) had evolved before the diversification of the Anguimorpha or it appeared only after a subdivision of the anguimorphan stem, the primitive, variable skull covering (fig. 28.2) being initial for both Diploglossa and Platynota (fig. 28 B). The platynotan type of covering would be morphologically derived by secondary disintegration of the shield in the first case (A). According to the alternative hypothesis (B), the small-plate pattern of the osteodermal skull covering of Platynota would be a continuation of the primitive ridge and furrow type organized into small rounded or polygonal elements by simple growth. The second hypothesis being more parsimonious it would be considered as a basis for a further discussion.

Exactly the same alternative may be proposed regarding the time of development of a shield type of the osteodermal skull covering of Scincomorpha. Since it is absent from the Late Jurassic representatives (HOFFSTETTER 1967) of the infraorder as well as from the Late Cretaceous Lance Formation (ESTES 1964) from most of the extant teiids and from the Late Cretaceous Macrocephalosauridae and Polyglyphanodontidae (SULIMSKI 1975), it is more likely subsequent to a diversification of the infraorder than antecedent to this process. It follows that the shield covering present in Scincomorpha and that of Anguimorpha should be called parallel rather than homologous, because they are probably not inherited from the common ancestor but only develop in connection with such a common inheritance — the shield type of squamation (fig. 28.1). Since, however, this connection is so close that the first of these characters may be considered a manifestation of the second, this parallelism reflects relationships, under a condition that the first supposition of the shared derived character of the shield-type of squamation will prove to be true.

According to the cladogram in fig. 28 B the type of squamation (1, 1′, 1″) is given a leading role in the evolution of the dermal skull covering of Platynota. However, the antecedence of the small-element squamation relative to small-element osteodermal covering cannot be positively stated in this section of the phylogeny. Both, the true dermal and the epidermal skull covering have been influenced by the same complex of factors, which is presumed to include size increase, frontal constriction, and development of mesokinetic mobility. At the early platynotan stage of evolution, or a necrosaurian grade (p. 69), the first two of these factors were probably strongly variable and so was the armour. The increasing skull kinesis and total body agility connected with predatory habits have probably been responsible for a modern platynotan tendency to the loss of the dermal armour.

Apart from the case of the Platynota, and quite independent from it and from each other, the small-plate osteodermal covering of the skull roof appeared twice within the anguimorphan group, in the Xenosauridae and in the Glyptosaurini. Although it has been positively shown

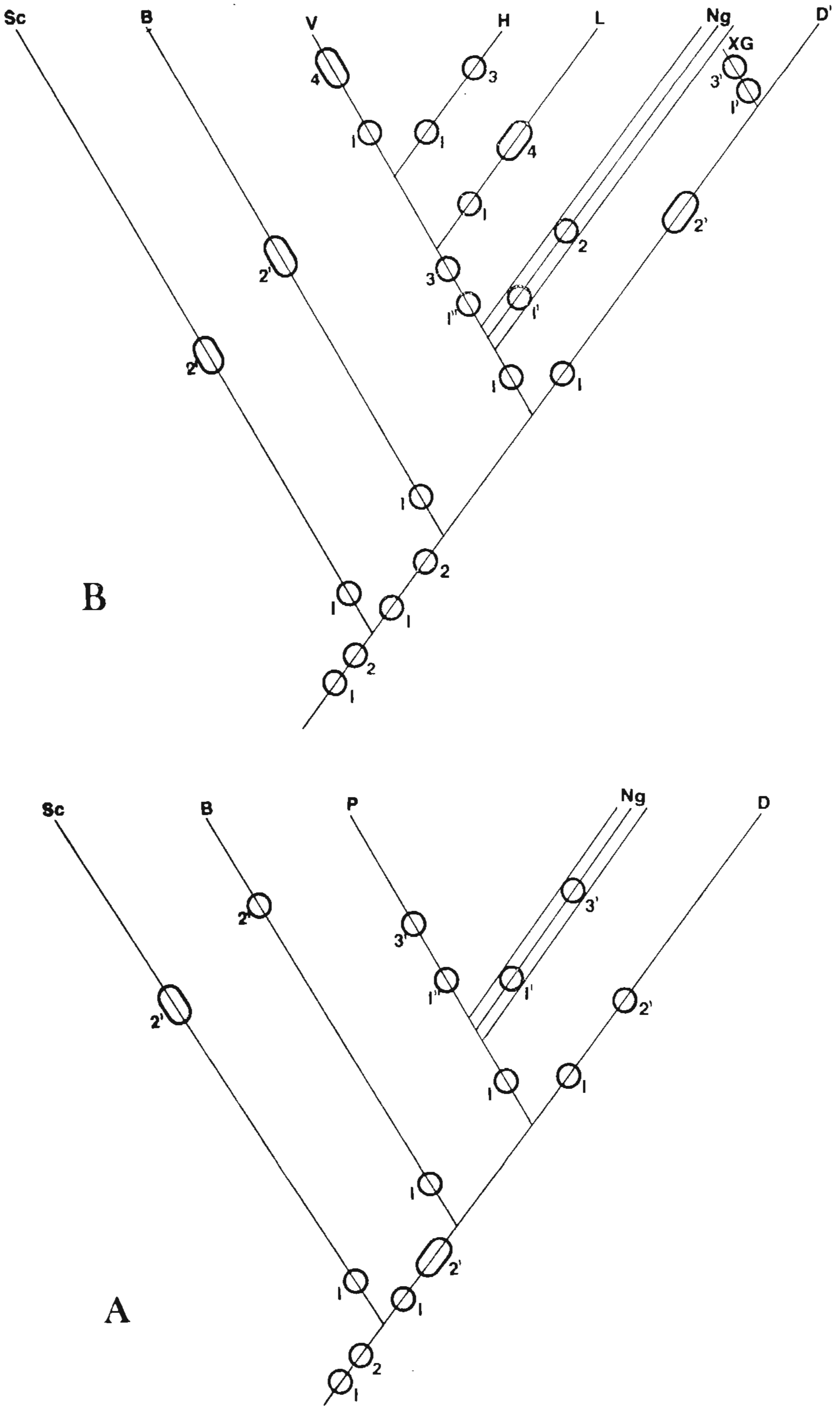


Fig. 28

Cladograms illustrating a distribution of character states of the skull covering within the autarchoglossan stem. A, B are the alternative hypotheses differing in the rate of stabilization of the osteodermal skull coverings. Some identical parts of the hypotheses are omitted in A. Circles denote different states of the dermal skull covering. Ovals denote the states considered to be a result of parallelism. *1*, *1′*, *1″* states of squamation; *1* shield pattern; *1′* pattern variable at a generic level; *1″* small-element pattern; *2-4* states of osteodermal skull covering; 2 pattern variable at the generic level, *2′* shield pattern; *3* primary small plate pattern; *3′* small-plate pattern developed by multiplication process; *4* reduced osteodermal skull covering. Sc — Scincomorpha, B — Bainguidae, L — Lanthanotidae, Ng — families of the necrosaurian grade, X+G — Xenosauridae and Glyptosaurini (not distinguished from one another by this method), D — Diploglossa, D′ — remaining Diploglossa, P — remaining Platynota.

only in the second case (see e. g. MESZOELY 1970), the small-plate pattern was probably secondary in both these groups. I would suppose that a drastic constriction of the frontals along with their deflection between the protrudent orbital borders have caused a multiplication of the armour in the Xenosauridae — the case of closing together the segmentation zones.

Most of the recent authors dealing with the Glyptosaurinae (MESZOELY 1970, MESZOELY, ESTES and HAUBOLD 1979, SULLIVAN 1979) agree that the small-element pattern displayed by the genus *Glyptosaurus* and its relatives (tribe Glyptosaurini SULLIVAN, 1979) is derivable from a shield pattern such as that of *Xestops* and *Arpadosaurus* (tribe Melanosaurini). On the basis of the universality of a tesselated pattern of dermal skeleton in different vertebrate groups as well as on CAMP'S (1923) opinion about the primitive character of the dermal skull covering consisting of uniform granular elements, SULLIVAN (1979) considered the skull armour of the *Glyptosaurini* as primitive and derived at the same time and he concluded by treating it as paedomorphic. The misunderstanding stems from the premise that the uniform granular elements mentioned by CAMP (1923) were the small polygonal elements of the tesselated pattern. In spite of their universality among the vertebrates, the tesselated pattern is by no means an early ontogenetic stage but rather a final stage of a dermal covering consisting of uniform small elements increasing by circumferential growth. In my opinion, the small-plate pattern of the osteodermal skull covering of the melanosaurinid ancestor of the *Glyptosaurini* has changed according to the changes of its craniological features, owing to the elasticity of the dermal armour already mentioned. Large body size which is said to be characteristic of the *Glyptosaurini*, resulting in a reduced contact between skull bones and the epidermis is suggestive of being a main cause of these changes. A tendency to a loosening of fusion between the dermal armour and the underlying bones stated by SULLIVAN (1979) in glyptosaurinin sequence: *Eoglyptosaurus* and *Paraglyptosaurus* (about the Middle Eocene), *Glyptosaurus* (Late Eocene) and *Helodermoides* (Uppermost Eocene and Oligocene) tends to support the above. However, the transition from the Melanosaurini to the Glyptosaurini is not documented by any exact body size data. My impression is that at least some of them have been the size of gerrhosaurid and lacertid specimens I have at my disposal (about 40 mm of skull length), while differing from them in the osteodermal covering pattern. I would suggest that the type of skull kinesis characterized by a perfectly preserved mesokinetic axis (see e. g. *Paraglyptosaurus princeps* SULLIVAN 1979, figs. 6, 7) has been a second factor favouring a transition to a small-element pattern differing from that of Gerrhosauridae and Lacertidae, which usually have this axis invaded by frontoparietal scutes.

Mandible

The main tendencies occurring in the evolution of the mandible of Anguimorpha and especially of the Platynota have been extensively discussed by MCDOWELL and BOGERT (1954). As documented by the present material, the most primitive representative of the Platynota, the necrosaurian *Proplatynotia* (p. 34) differs from the Diploglossa by a loosening of a contact between the dentary and the splenial, and between the dentary and the coronoid as well as by a straightening of the suture between the dentary and the supraangular. The straightening of this suture is partly connected with a horizontal elongation of the anterior ramus of the coronoid and a corresponding shortening of the upper part of the dentary. Although a true intramandibular joint is not yet developed in the *Proplatynotia*, some amount of abductive movement has been permitted by these changes in bone disposition. A posterior extent of the splenial, which has been quite significant in *Proplatynotia* (although it did not attain the level of the coronoid apex as it does even in the Diploglossa) has been subject to variability over most of the platynotan phylogeny. It becomes reduced and aligned with the anterior margin of the coronoid only in some specialized platynotan groups: the Lanthanotidae and the Mosasauridae. Contrary to the opinion of McDowell and Bogert (1954), I consider the structure of the intramandibular joint in these groups as parallel formations caused by a further development of lateral mobility of the mandible based on the same structural foundation inherited from the earliest platynotans. The anterior extent of the splenial is reduced to about half the length of the dentary in *Proplatynotia* and to about 1/3 of the dentary length in the Diploglossa.

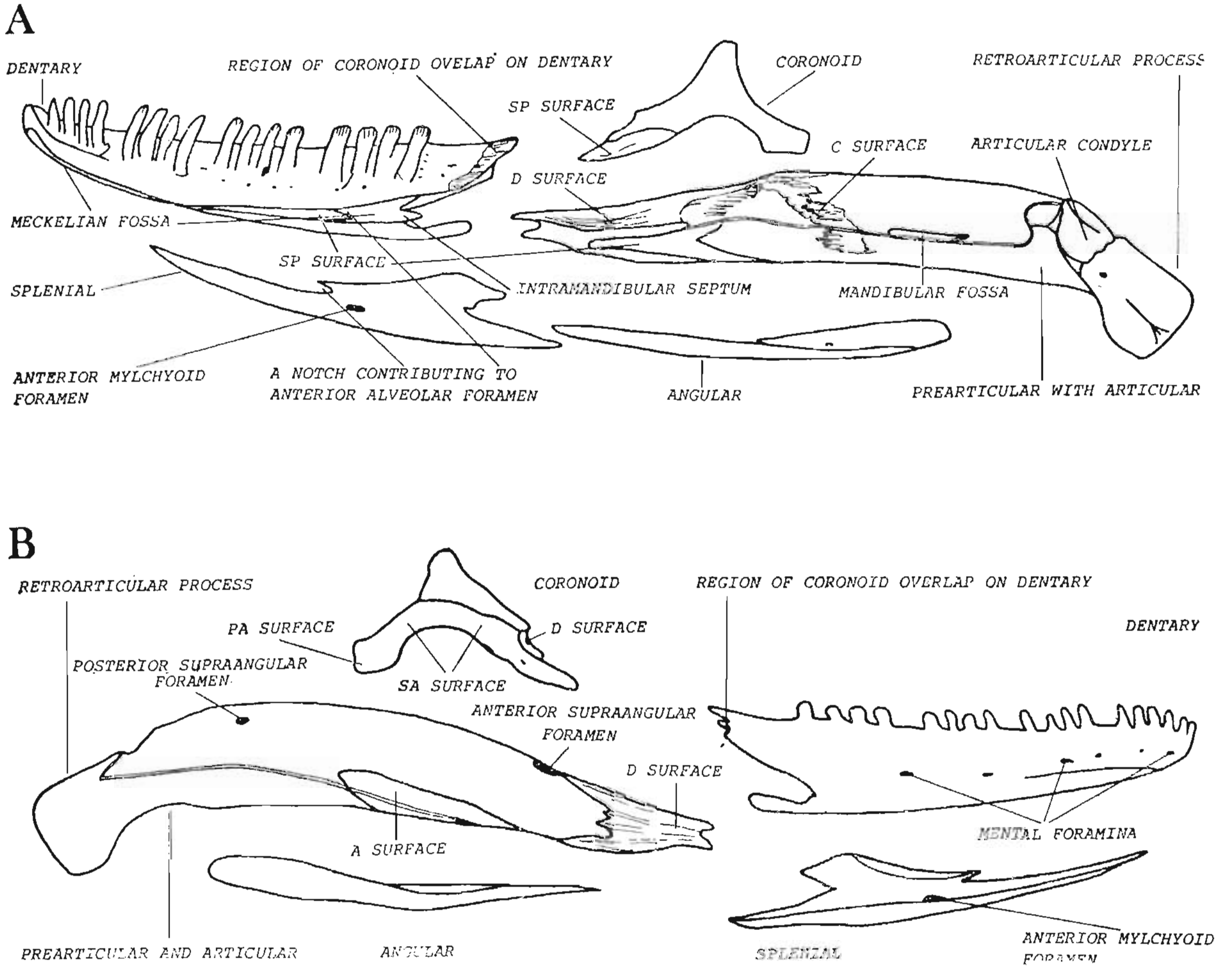


Fig. 29

Disengaged bones of a mandible of a juvenile specimen of *Gerrhonotus leiocephalus* ZPAL z. p. R-I/12 demonstrating surface of overlap of the following bones on their neighbours: A — angular; C — coronoid; D — dentary; PA prearticular and SP splenial. A — Medial view. B — Lateral view. Not to scale.

Anterior reduction of the splenial is thus considered shared derived for the modern superfamilies of Anguimorpha, the Diploglossa and the Platynota, whereas a full length development of this bone is considered a plesiomorphic character state. The course of the sutures between the bones of the fossil mandibles which are basic for a determination of their evolutionary level has very often to be reconstructed from the traces of bones left on the neighbouring ones, as shown by disengaged mandibular elements of *Gerrhonotus leiocephalus* (fig. 29, pl. 10 : 3). The surface of the following bones are the most indicative of the state of the intramandibular joint: the surface of overlap of the dentary on the surangular; of the splenial on the prearticular and of the coronoid on the dentary (see fig. 29).

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EXPLANATIONS OF THE PLATES 1—13

PLATE 1

Paravaranus angustifrons gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/67 — holotype

1a. The skull in dorsal view.
1b. The same in occipital view.
1c. The same in ventral view.
1d. A detail of the right tooth row in ventromedial view.

1c. A detail of the right brain case wall in ventrolateral view.
2. The left mandible of the holotype in medial view.

All stereo-photographs, × 3
(see also text-figs. 2, 3, 4A and plate 4 : 1)

Varanus griseus

Recent, UW, unnumbered specimen

3. Stereo-photograph of the skull in occipital view, × 1.

Tupinambis sp.

Recent, HUB 1050/35588

4. Stereo-photograph of the skull in occipital view, × 1.

Photo: E. Wyrzykowska

PLATE 2

Bainguis parvus gen. n., sp. n.

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia, ZPAL MgR-I/46 — holotype

1a. The skull in dorsal view.
1b. The same in left side view.
1c. The same in right side view, partly prepared.
1d. The same in right side view with right quadrate and posterior part of right mandible removed.

All stereo-photographs, × 3

2. Stereo-photograph of the vertebral column of MgR-II/11, × 1.5.

(See also text-figs. 4C, 5, 6; plates 3 and 13 : 5)

Gobiderma pulchra gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia, ZPAL MgR-III/66

3. Stereo-photograph of the rostral part of the skull in ventral view, × 2.

(See also plate 6 : 2 and 7 : 3)

Cherminotus longifrons gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia

4. A detail of the holotype, ZPAL MgR-III/59; the brain case in left side view. Stereophotograph, × 6.

(See also plate 11 : 3c)

Photo: E. Wyrzykowska

PLATE 3

Bainguis parvus gen. n., sp. n.

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia

1a. The partly prepared skull ZPAL MgR-I/46, the holotype, in ventral view.
1b. The same with quadrate and posterior part of right mandible removed to show the brain case wall; ventral view.

1c. The same in occipital view.
2a. The anterior part of the right mandible of the holotype in medial view.
2b. The same in lateral view.
3a. The juvenile skull ZPAL MgR-I/90 with the mandible in ventral view.
3b. The same in right side view.
3c. The same in dorsal view.

All but 2b stereo-photographs, all × 3
(see also text-figs. 4C, 5, 6 and plate 2)

Photo: E. Wyrzykowska

PLATE 4

Paravaranus angustifrons gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/67 — holotype

1a. The skull in left side view, × 4.5.
1b. The same in right side view, × 3.

Both stereo-photographs
(See also text-figs. 2, 3, 4A and plate 1 : 1, 2)

Proplatynotia longirostrata gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/68 — holotype

2a. The skull in left side view.
2b. The same in right side view.
5a. The brain case of the same in left side view.
5b. The basisphenoid + parasphenoid in front view.

All stereo-photographs, × 2
(See also text-figs. 4B, 8, 9A and plates 5 : 1, 2; 7 : 4 and 13 : 4)

Gobiderma pulchra gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia, ZPAL MgR-III/65

3. Stereo-photograph of the brain case in left side view, × 2.

(See also plates 2 : 3; 6 : 1—4; 7 : 1—3; 9 : 2 and 13 : 3)

Anguis fragilis

Recent, ZPAL R-I/6, juvenile specimen

4. Stereo-photographs of the brain case in ventral view, × 4.

Photo: E. Wyrzykowska

PLATE 5

Proplatynotia longirostrata gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/68 — holotype

1a. Stereo-photograph of the skull in dorsal view.
1b. Stereo-photograph of the same in ventral view.

2. The right mandible of the holotype in lateral view.

All × 2

(See also text figs. 4B, 8, 9A and plates 4 : 1, 5; 7 : 4; 13 : 4)

Parviderma inexacta gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/43 — holotype

3. The fragmentary skull in left side view.
4. The left mandible in medial view.

Stereo-photographs, × 3

(See also text-figs 9F, 10 and plates 6 : 5, 13 : 2)

Xenosaurus grandis

Recent, MCZ 46785

5. Stereo-photographs of the left mandible, × 2.

Photo: E. Wyrzykowska

PLATE 6

Gobiderma pulchra gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia

1. Stereo-photograph of the skull of the holotype, ZPAL MgR-III/64, in dorsal view, × 1.5.

2a. The skull of the specimen ZPAL MgR-III/66 in dorsal view, × 2.

2b. The detail of the same. Ornamentation of the frontal, × 4.

3a. The skull of the specimen ZPAL MgR-III/65 in dorsal view, × 1.5.

3b. A fragment of the right mandible of the same, with a tooth, medial view, × 2.

(See also text-figs. 4D, 9C, 11 and plates 7 : 1, 2 : 3, 9 : 2, 13 : 3)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia

4. Stereo-photograph of a skull fragment of the specimen ZPAL MgR-I/54 in dorsal view, × 1.5.

Parviderma inexacta gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/43 — holotype

5. Stereo-photograph of the skull in dorsal view, × 2.8.

(See also text-figs. 9F, 10 and plates 5 : 3, 4; 13 : 2)

Xenosaurus grandis

Recent, MCZ 46785

6. Stereo-photograph of the skull in dorsal view, × 2.

Gerrhonotus leiocephalus

Recent, ZPAL R-I/12 — a juvenile specimen

7. The fragmentary skull roof in dorsal view, × 2.5.

Ophisaurus apodus

Recent, HUB 42402

8. The skull in dorsal view, × 2.

Photo: E. Wyrzykowska

PLATE 7

Gobiderma pulchra gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia

1a. Stereo-photograph of the skull of the holotype ZPAL MgR-III/64 in ventral view, × 1.5.
1b. Stereo-photograph of the same in left side view, × 1.5.
2a. The right mandible of the holotype in lateral view, × 1.5.
2b. Stereo-photograph of the same in medial view, × 1.5.
3. The right mandible of the specimen ZPAL MgR-III/66 in medial view, × 3.

(See also text-figs. 4D, 9C, 11 and plates 6 : 1—4; 9 : 2; 13 : 3)

Proplatynotia longirostrata gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-IIf/68 — holotype

4. Stereo-photograph of the right mandible in medial view, × 2.

(See also text-figs. 4B, 8, 9A and plates 4 : 2, 5; 5 : 1, 2; 13 : 4)

Heloderma sp.

Recent, ZPAL R-I/4

5a. The mandible in medial view, × 1.5.
5b. The same in lateral view, × 1.5

Photo: E. Wyrzykowska

PLATE 8

Saniwides mongoliensis gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/72 — holotype

1a. The skull in dorsal view, × 1.5.
1b. The same in ventral view, × 1.5.
2. The left mandible in medial view, × 2.
3a. The right mandible in medial view, × 2.
3b. The same in lateral view, × 2.

All but 3b stereo-photographs

(See also text-figs. 9E, 14 and plates 9 : 3, 4; 13 : 1)

Photo: E. Wyrzykowska

PLATE 9

Telmasaurus grangeri GILMORE, 1943

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/65

1a. The skull in dorsal view.
1b. The same in left side view.
1c. The same in occipital view.

All stereo-photographs, × 1.5.
(See also text-figs. 4G, 15, 16 and plate 10 : 1)

Gobiderma pulchra gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia, ZPAL MgR-III/64 — holotype

2. Stereo-photograph of the skull in occipital view, × 1.5.

(See also text-figs. 4D, 9C, 11 and plates 6 : 1-4; 7 : 1-3; 13 : 3)

Saniwides mongoliensis gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/72 — holotype

3. The skull in occipital view.
4. The brain case of the same in right side view.

Both stereo-photographs, × 1.5
(See also text-figs. 9E, 14 and plate 8)

Varanus griseus

Recent, UW unnumbered specimen

5. A detail of the skull in dorsal view, × 1.5.

Photo: E. Wyrzykowska

PLATE 10

Telmasaurus grangeri GILMORE, 1943

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/65

1a. The skull in ventral view.
1b. The brain case of the same in left side view.
1c. A detail of the skull in right side view.

All stereo-photographs, × 1.5.
(See also text-figs 4G, 15, 16 and plate 9 : 1)

Varanus griseus

Recent, UW unnumbered specimen

2. A detail of the skull in ventral view, × 1.5.

Gerrhonotus leiocephalus

Recent, ZPAL z. p. R-I/12 — a juvenile specimen

3a. Disengaged bones of the mandible in medial view.
3b. The same in lateral view.

All stereo-photographs, × 2.
(See also text-fig. 29)

Photo: **E. Wyrzykowska**

PLATE 11

Cherminotus longifrons gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia

1a. The fragmentary skull ZPAL MgR-III/67 in dorsal view.
1b. The same in right side view.
2a. The fragmentary left mandible of the same specimen in medial view.
2b. The same fragmentary left mandible in lateral view.
3a. The skull ZPAL MgR-III/59, the holotype, in right side view.
3b. The rostral part of the same in left side view, × 6.
3c. The same in left side view.

All but 2 and 3c stereo-photographs. All but 3c × 3
(See also text-figs 4E, 9G, 17 and plates 12 : 1, 2 and 2 : 4)

Lanthanotus borneensis

Recent, MCZ 8305

4a. The stereo-photograph of the skull in left side view reversed, × 2.8.
4b. The left mandible in lateral view, × 2.

Photo: **E. Wyrzykowska**

PLATE 12

Cherminotus longifrons gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia

1a. The skull of the holotype, ZPAL MgR-III/59, with a damaged rostral part, in dorsal view.
1b. The same in ventral view.
1c. A fragment of the rostral part of the same with a preserved left border, in dorsal view.
1d. The same in ventral view.
2. A detail of the skull ZPAL MgR-III/67 with the mandible *in situ*, in ventral view.

All but 1c and 1d stereo-photographs. All × 3
(See also text-figs 4E, 9G, 17 and plate 11 : 1-3)

Lanthanotus borneensis

Recent MCZ 8305

3a. The skull in dorsal view.
3b. The same in ventral view.

Both stereo-photographs × 2.8

Photo: E. Wyrzykowska

PLATE 13

Saniwides mongoliensis gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/72 — holotype

1. The skull in right side view, × 1.5.
(See also text-figs 9E, 14 and plates 8; 9 : 3, 4)

Parviderma inexacta gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-I/43 — holotype

2a. The fragmentary skull in ventral view, × 2.8.
2b. The mandible of the same *in situ*, × 2.8.
(See also text-figs 9F, 10 and plates 5 : 3, 4; 6 : 5)

Gobiderma pulchra gen. n., sp. n.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav, Gobi Desert, Mongolia, ZPAL MgR-III/64

3a. The lacrimal region of the skull in dorsal view, × 4.
3b. The postorbital region of the skull in dorsolateral view, × 4.
(See also text-figs 4D, 9C, 11 and plates 6 : 1-4; 7 : 1-3; 9 : 2)

Proplatynotia longirostrata gen. n., sp. n.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia, ZPAL MgR-III/68 — holotype

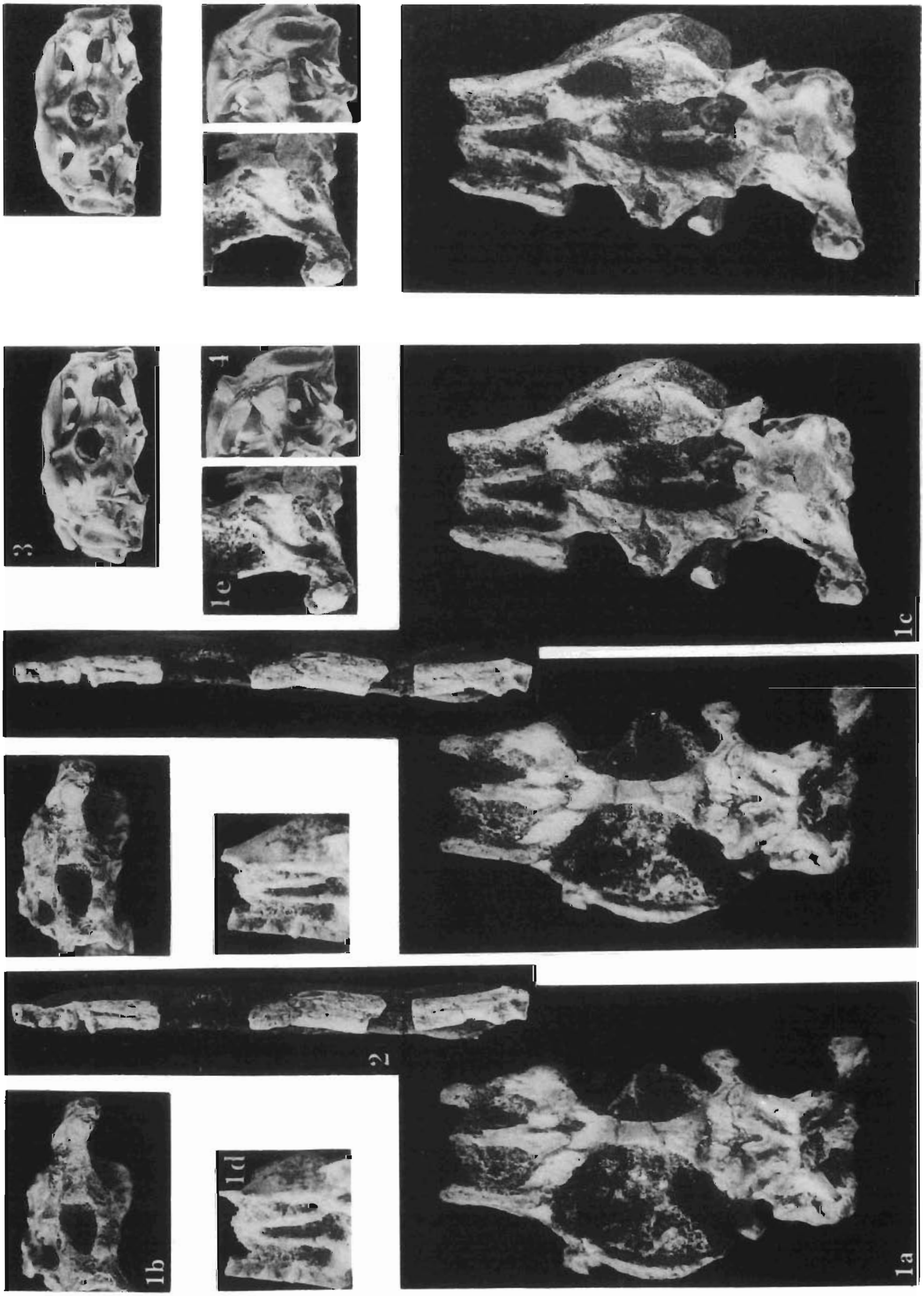
4. A detail of the skull in dorsolateral view, × 3.
(See also text-figs 4B, 8, 9A and plates 4 : 2, 5; 5 : 1, 2; 7 : 4)

Bainguis parvus gen. n., sp. n.

Upper Cretaceous, Djadochta Formation, Bayn Dzak, Gobi Desert, Mongolia, ZPAL MgR-II/10

5. Body osteoscutes, × 1.5.
(See also text-figs 4C, 5, 6 and plates 2, 3)
All but 2b stereo-photographs

Photo: E. Wyrzykowska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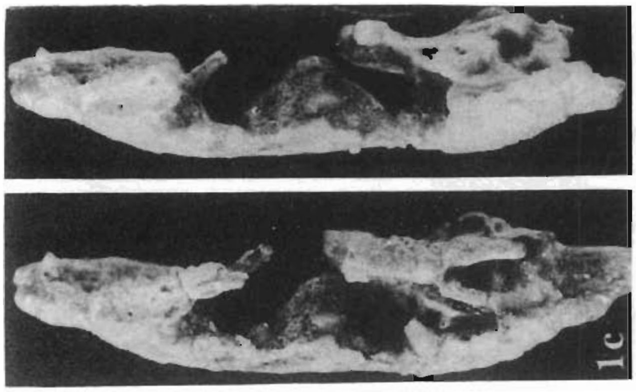
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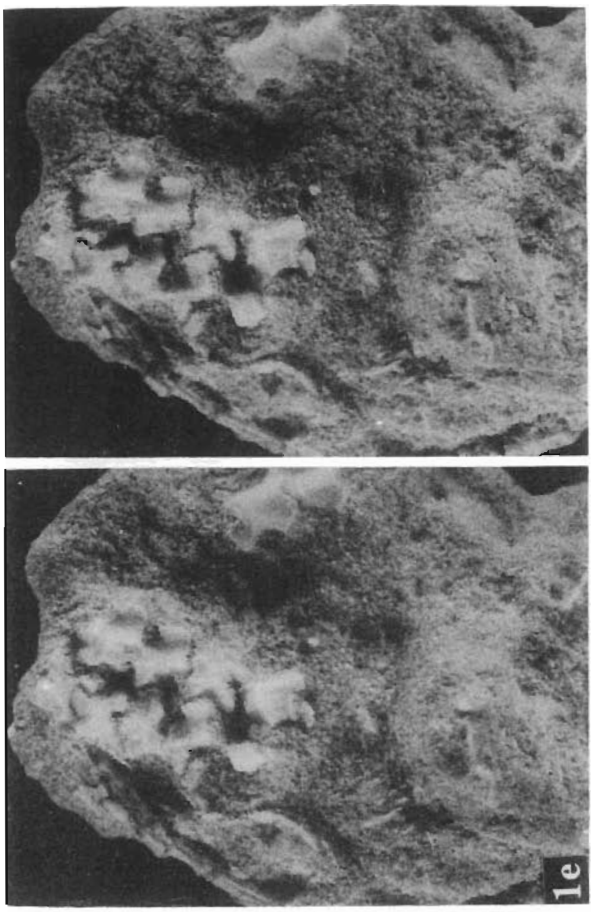
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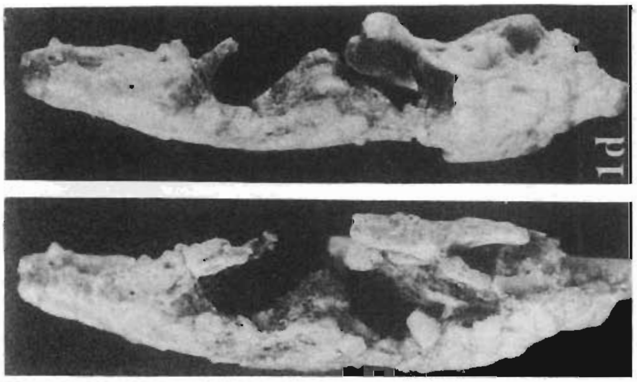
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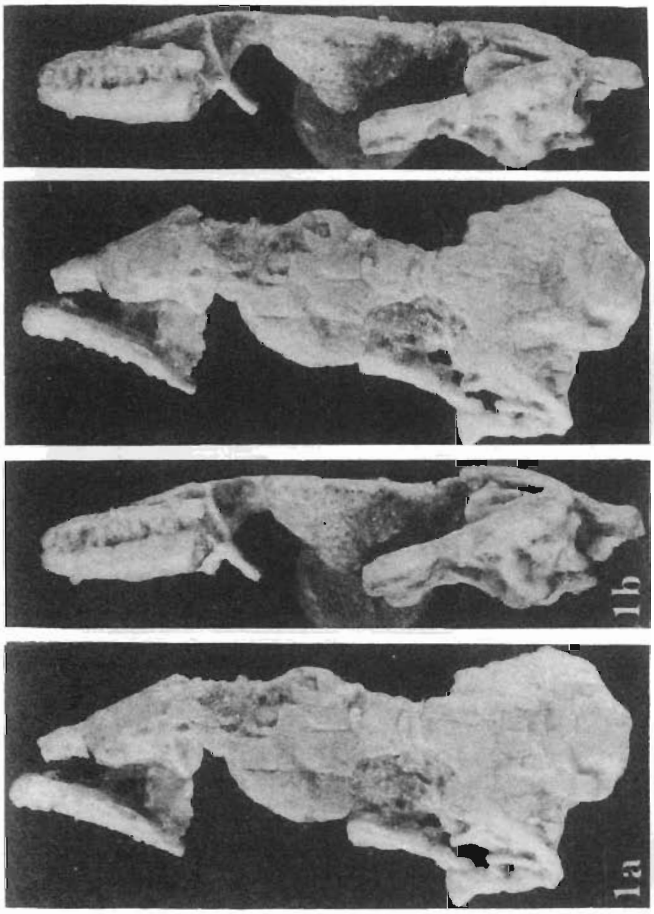
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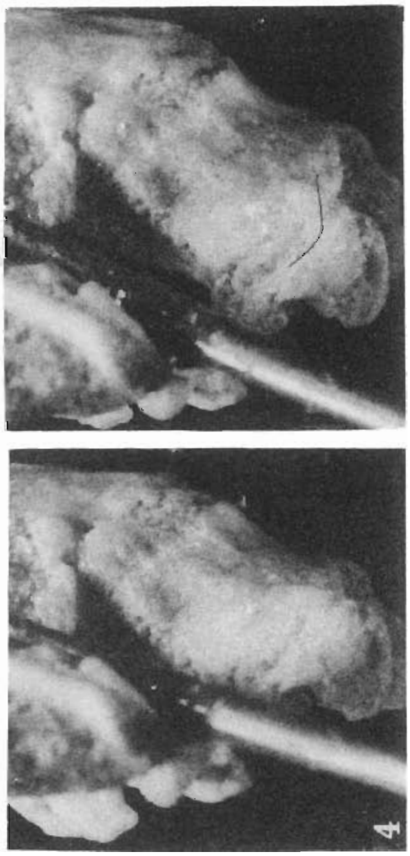
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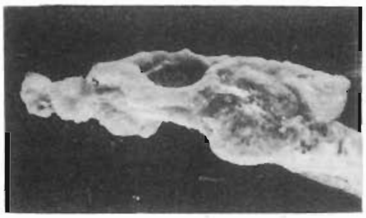

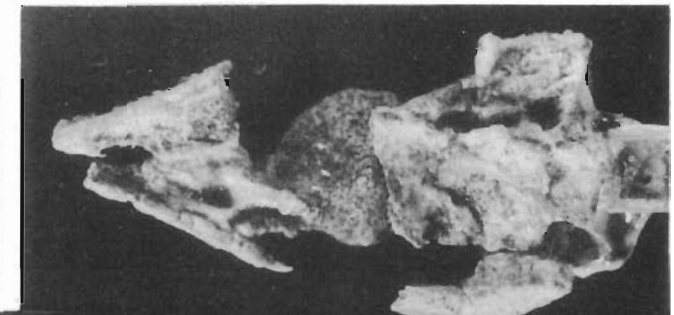

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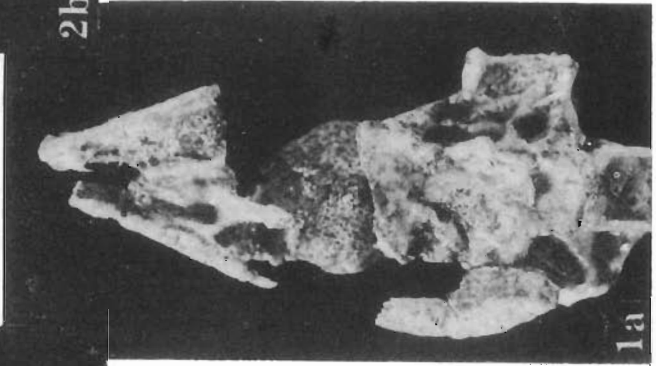

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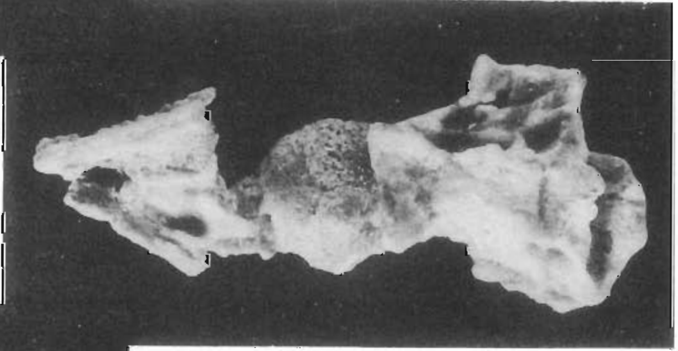

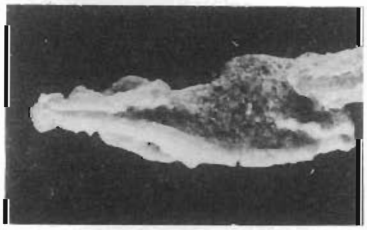

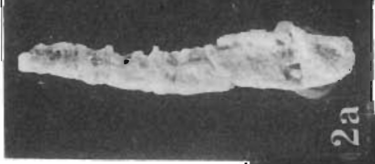

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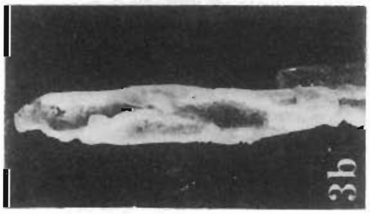

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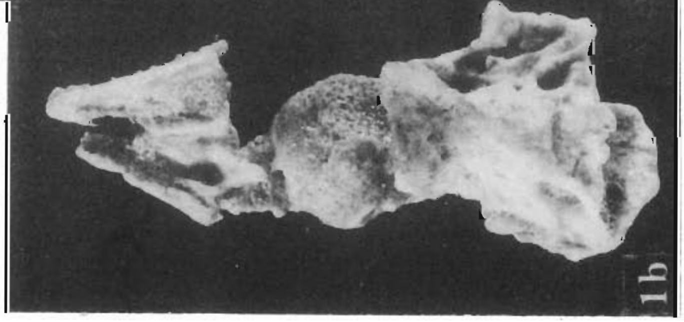

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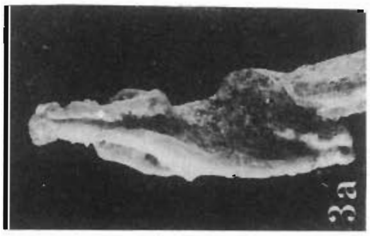

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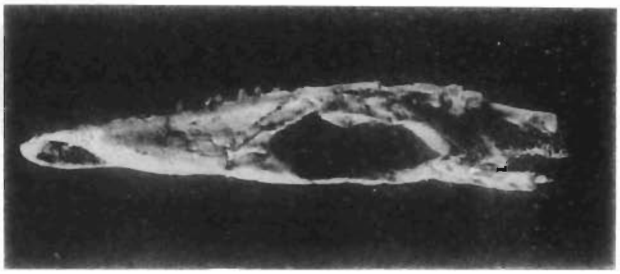

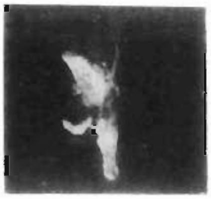

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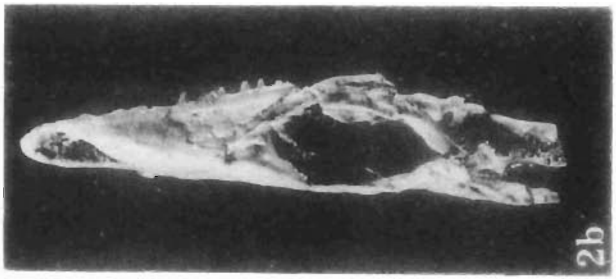

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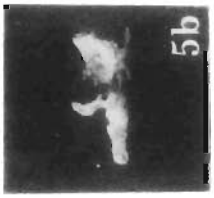

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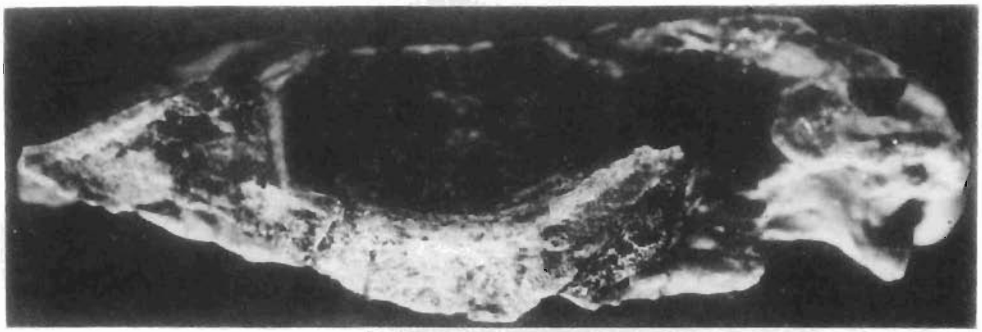

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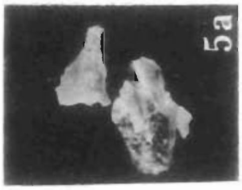

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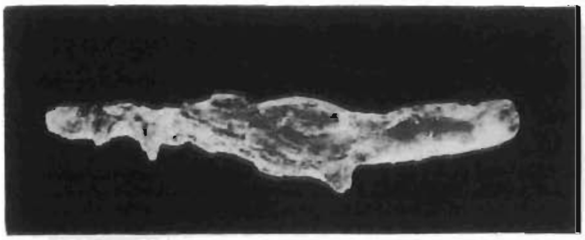

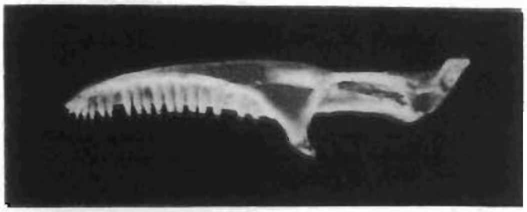

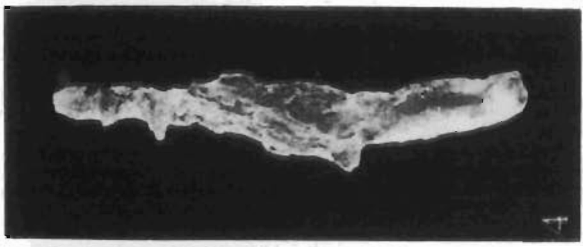
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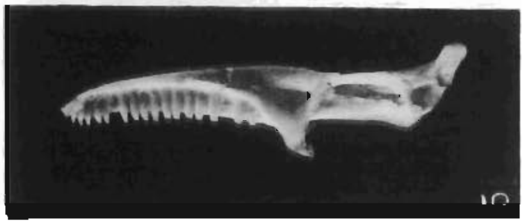
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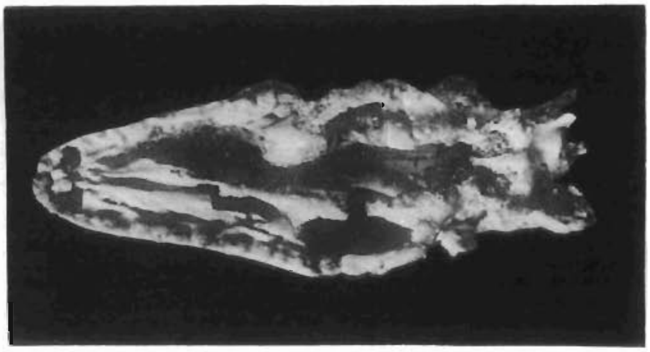

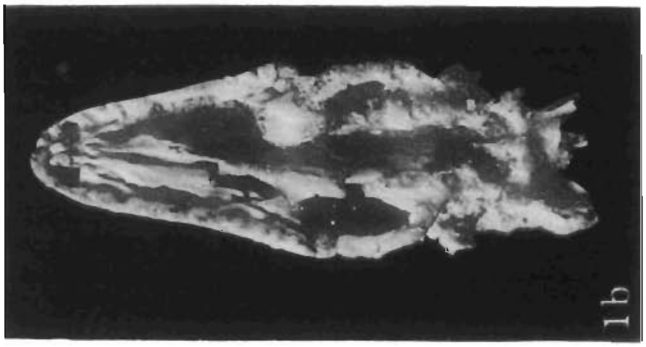
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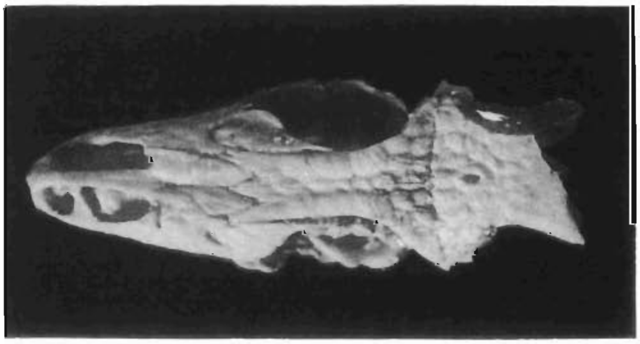

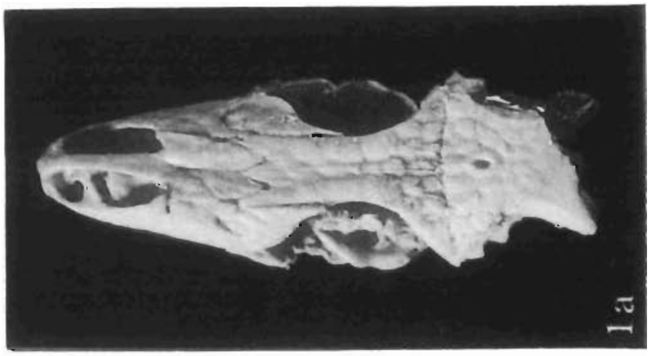
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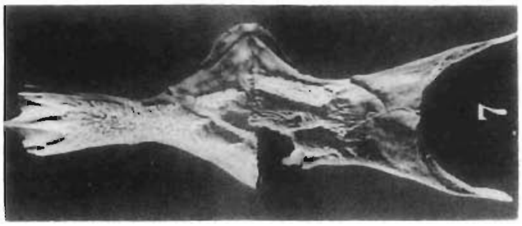
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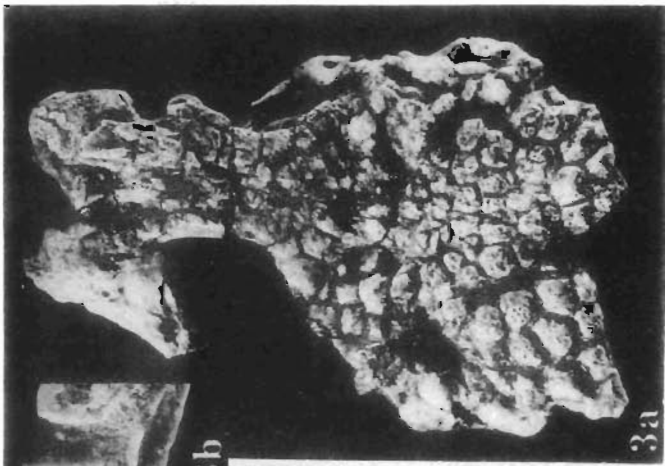
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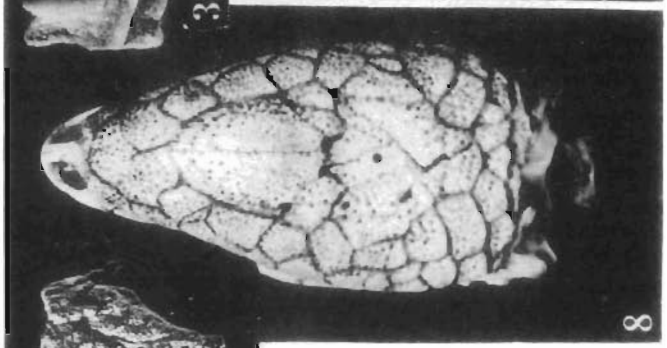
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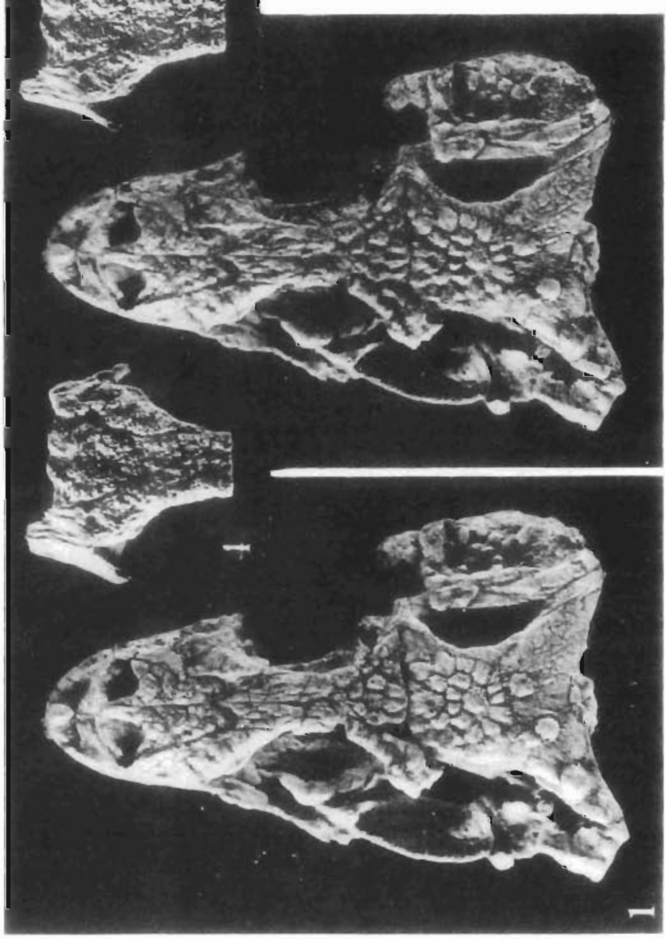
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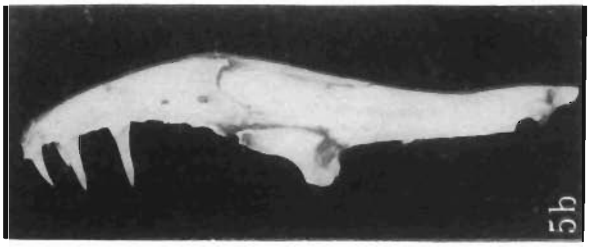
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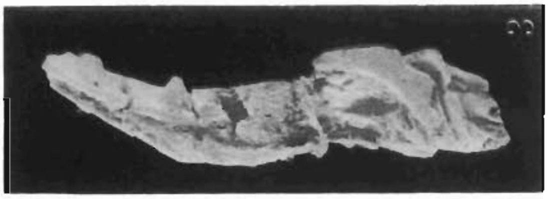
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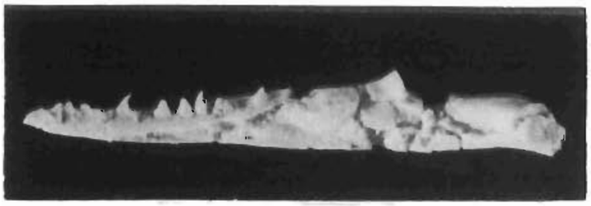

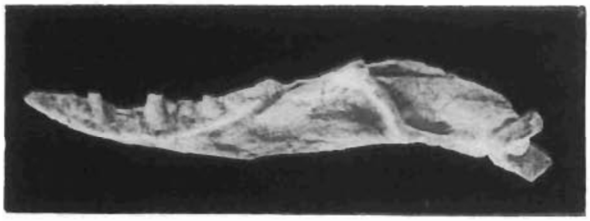

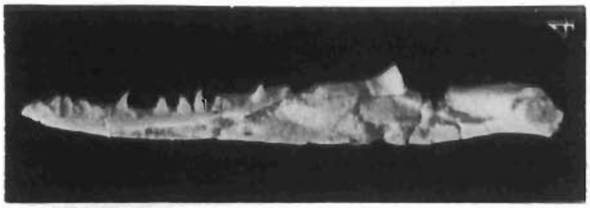
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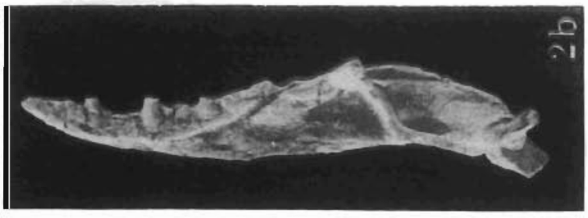
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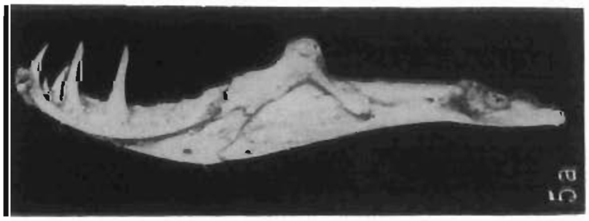
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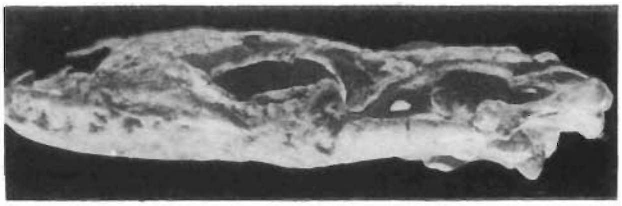


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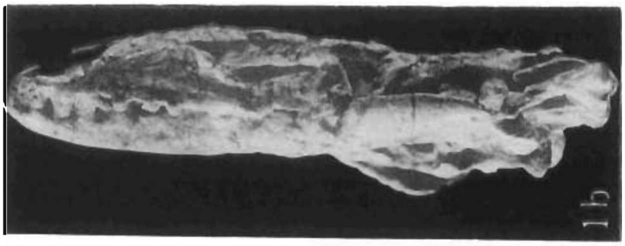
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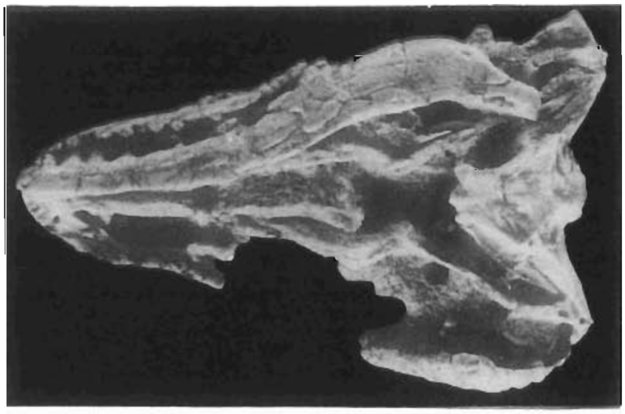

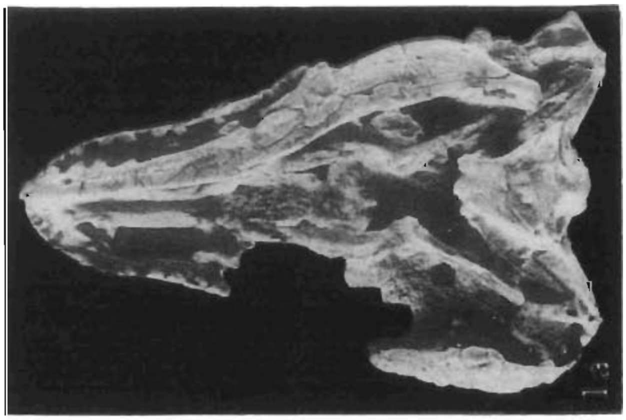
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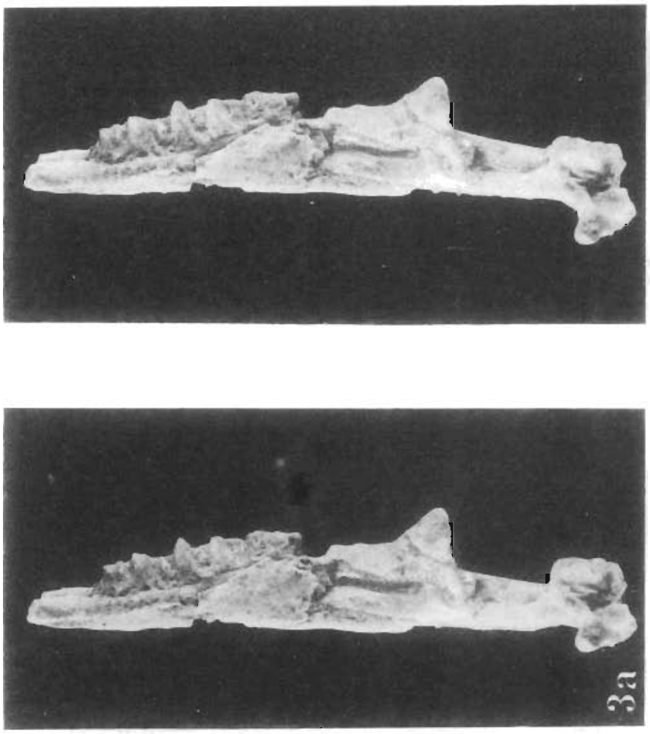
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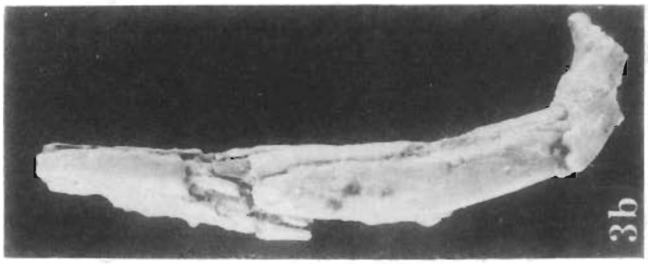
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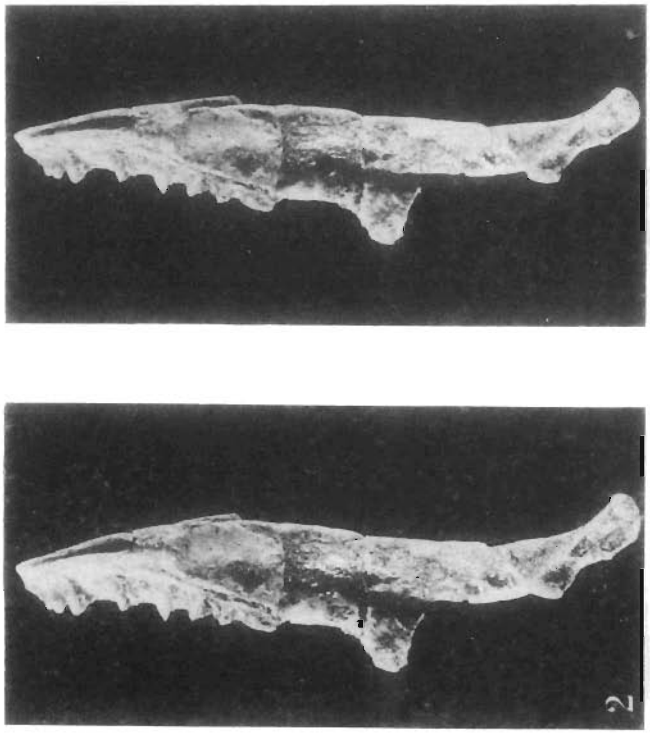
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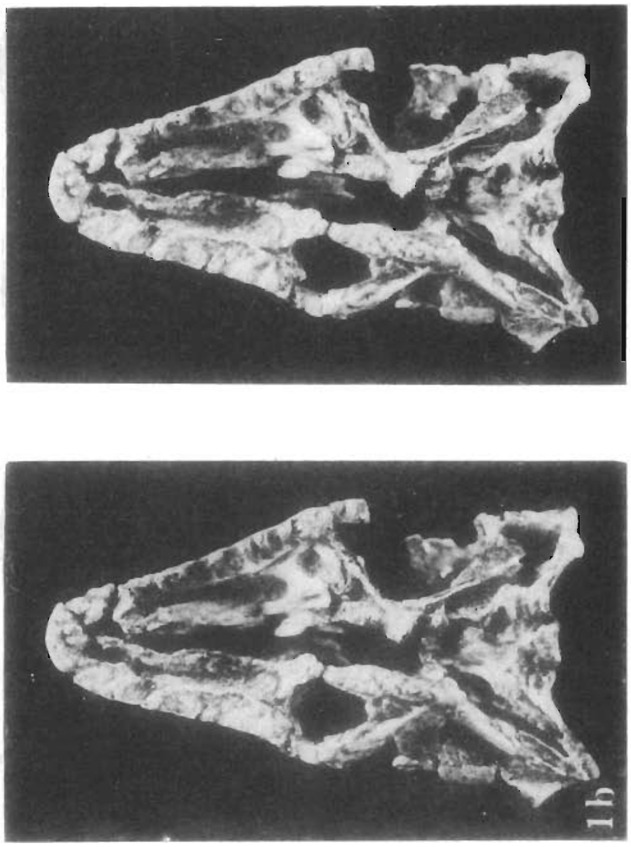
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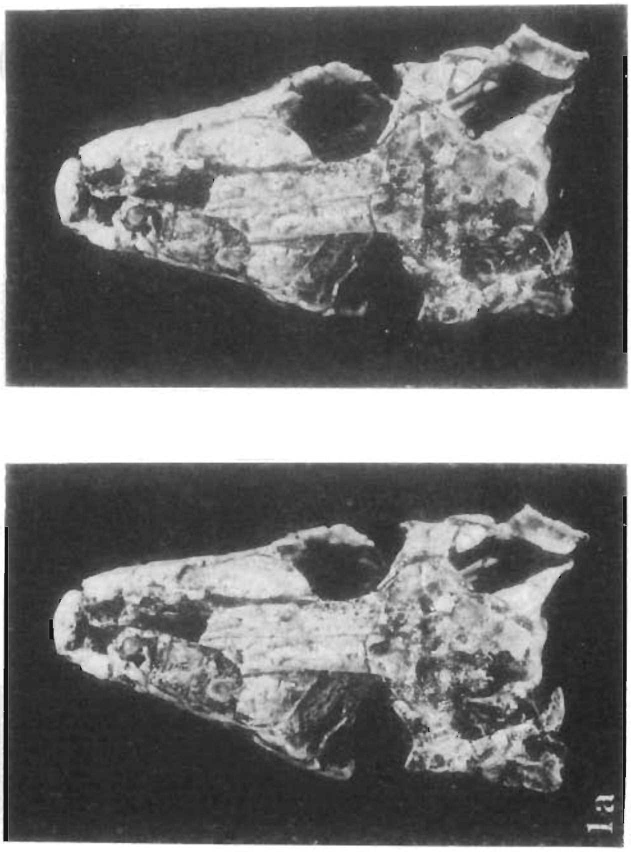
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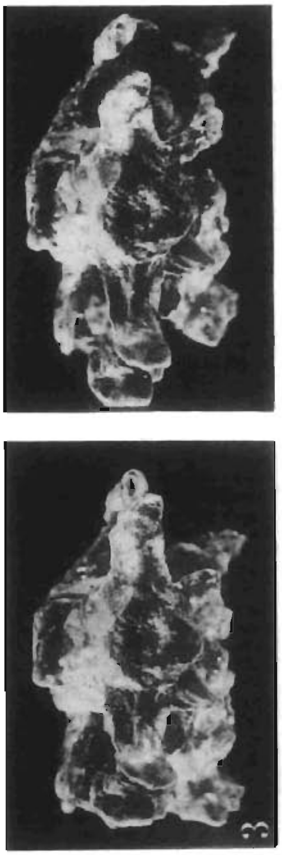

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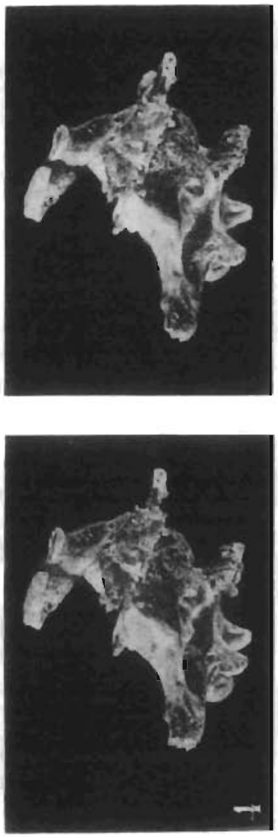

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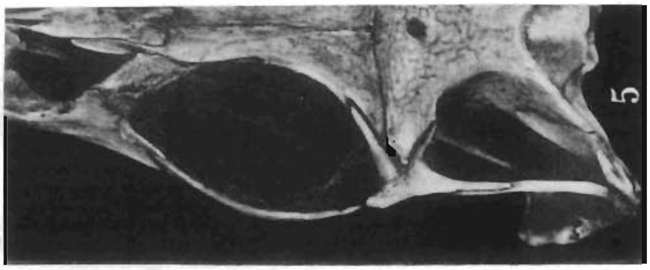

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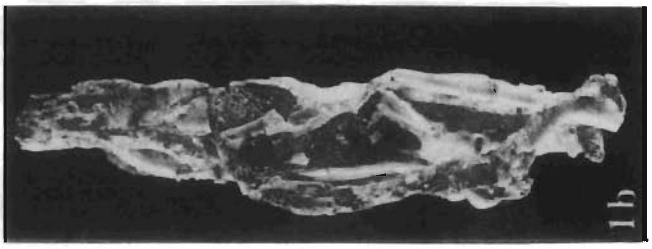

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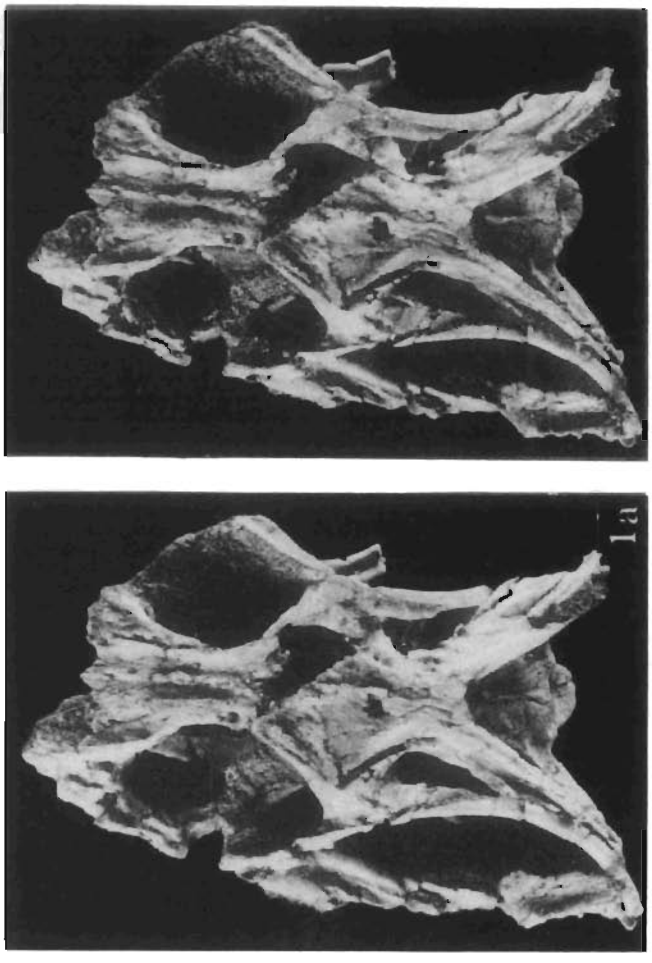

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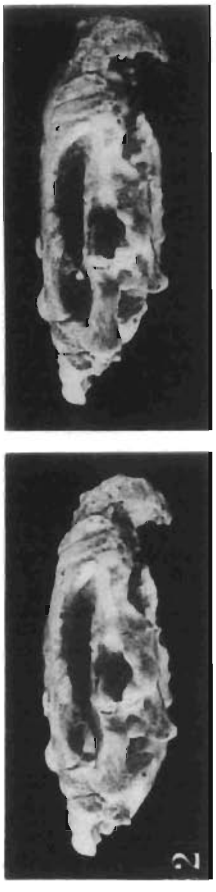

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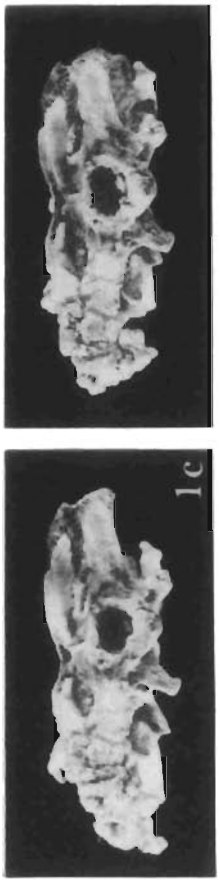

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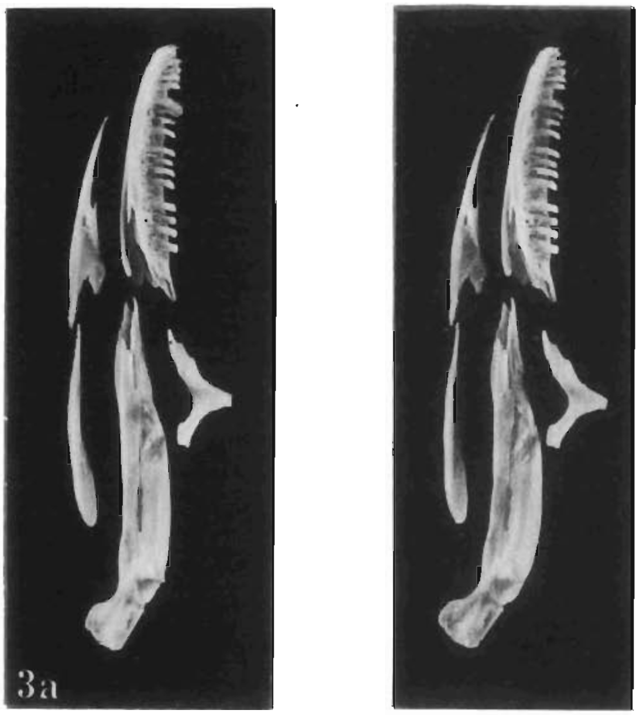
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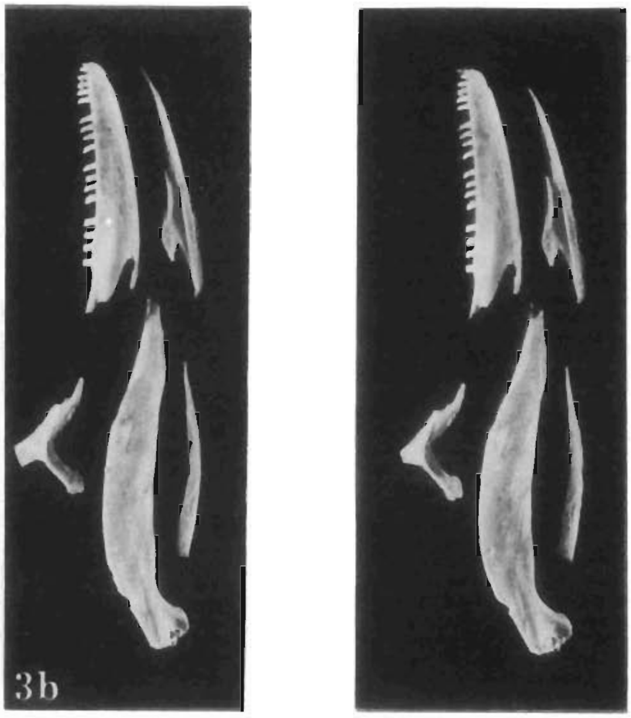
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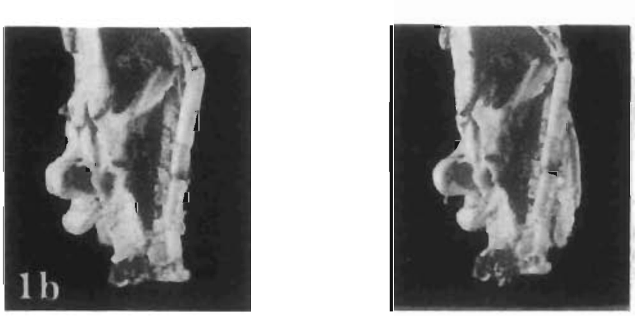
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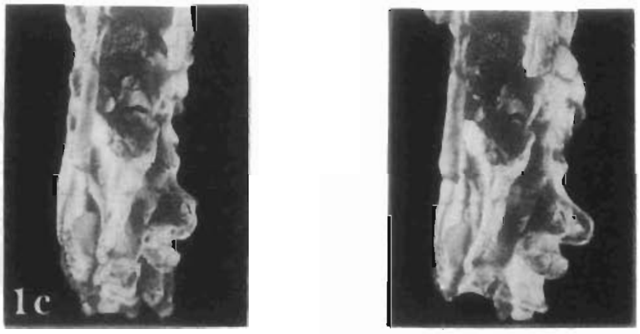
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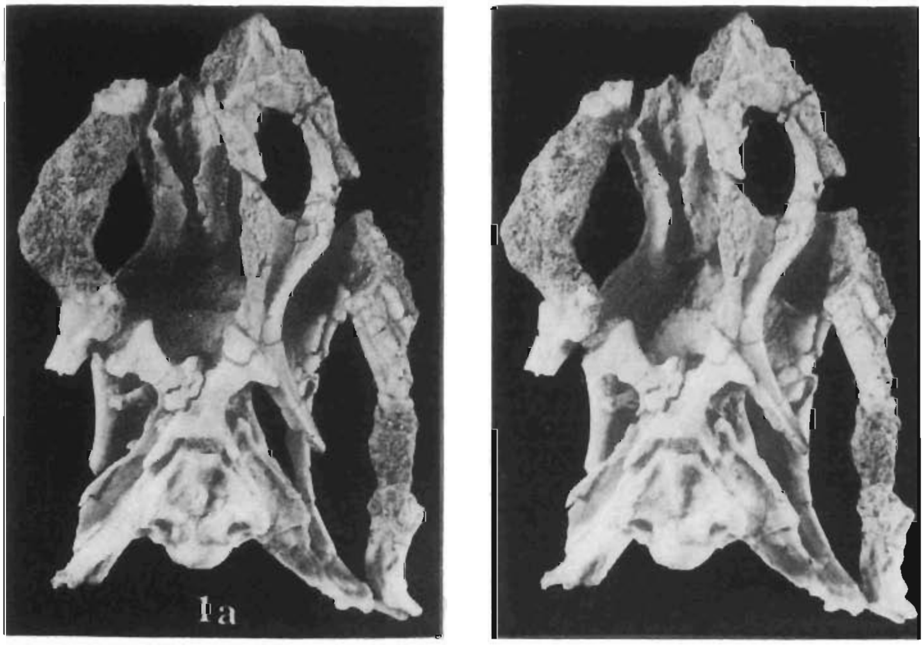
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2

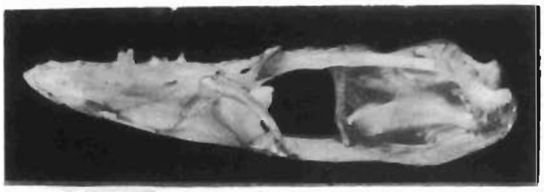

2a

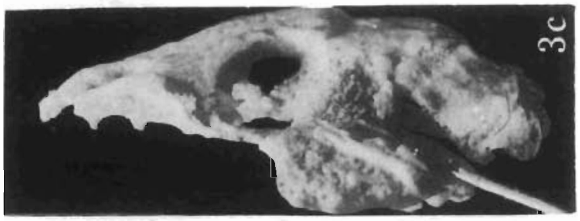

2b


4b


1b


3a

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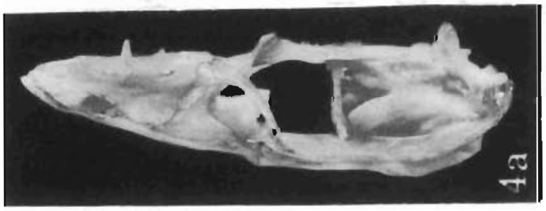
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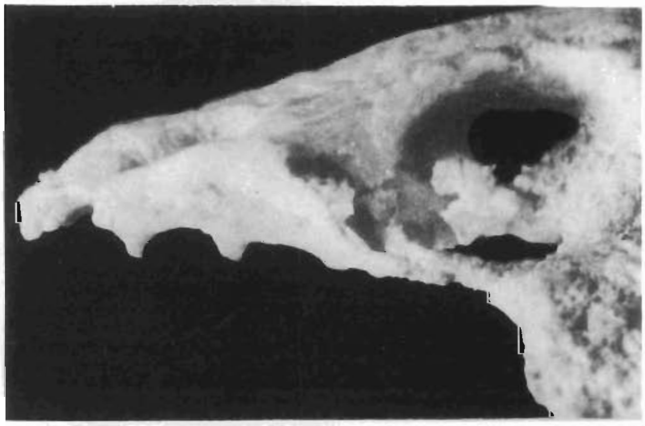


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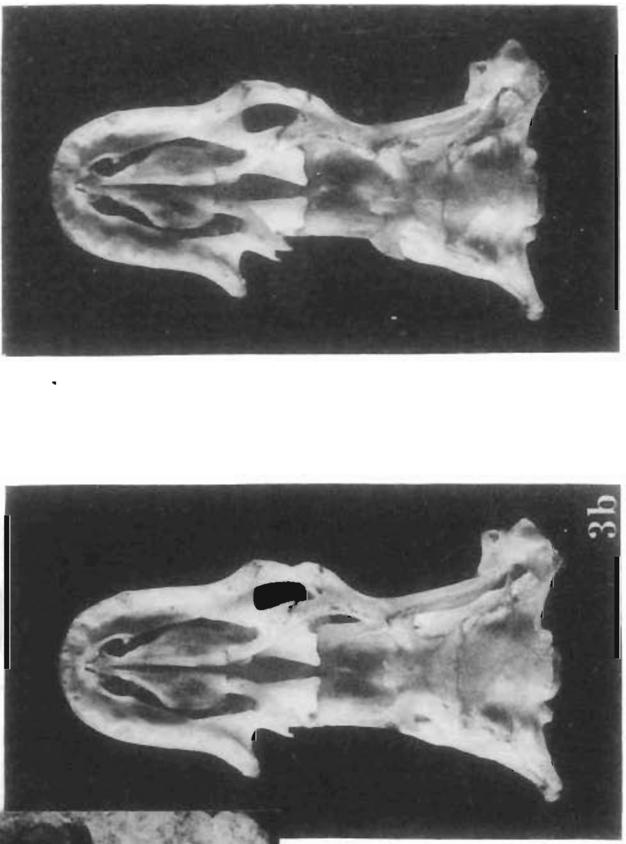
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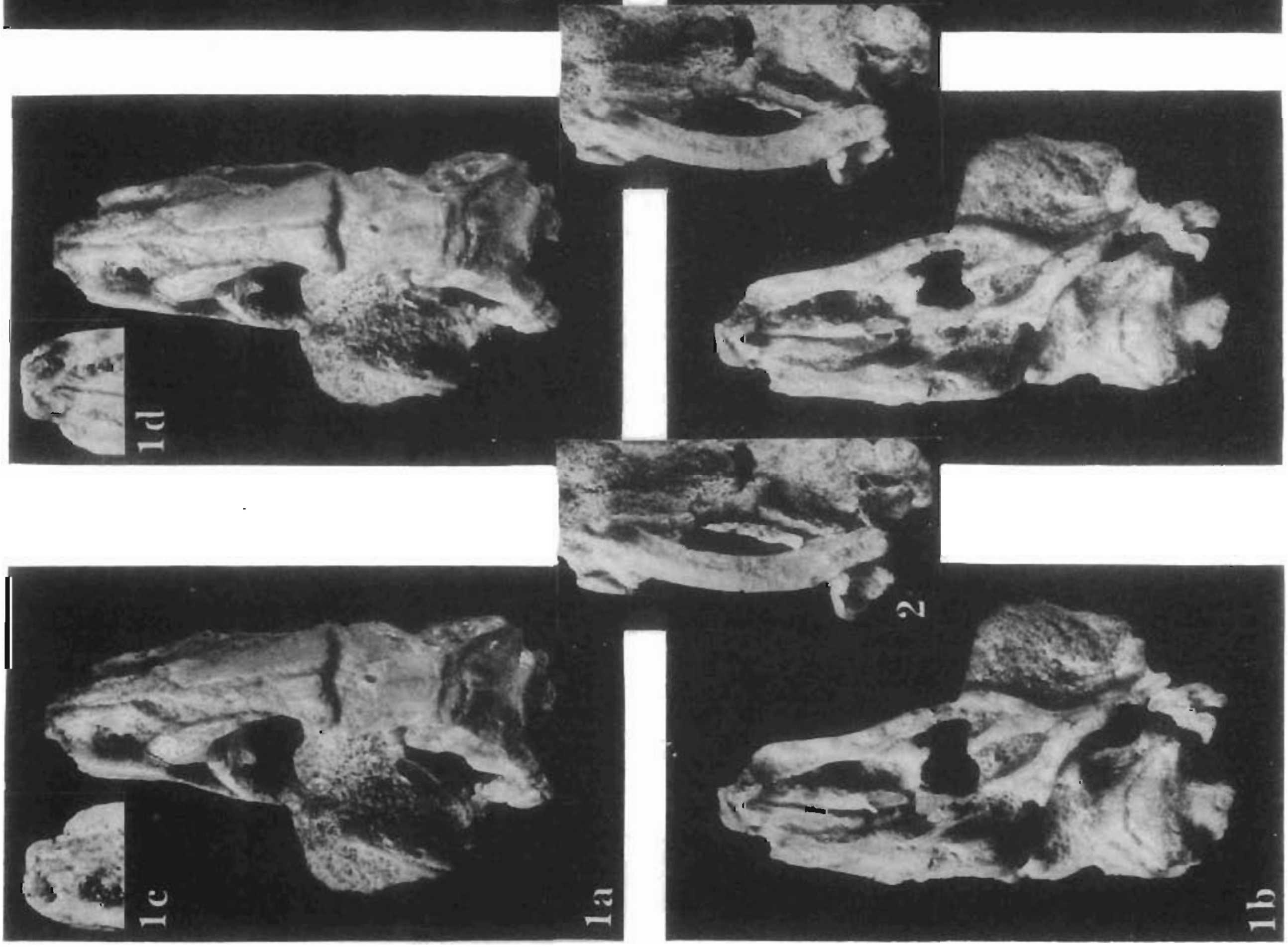
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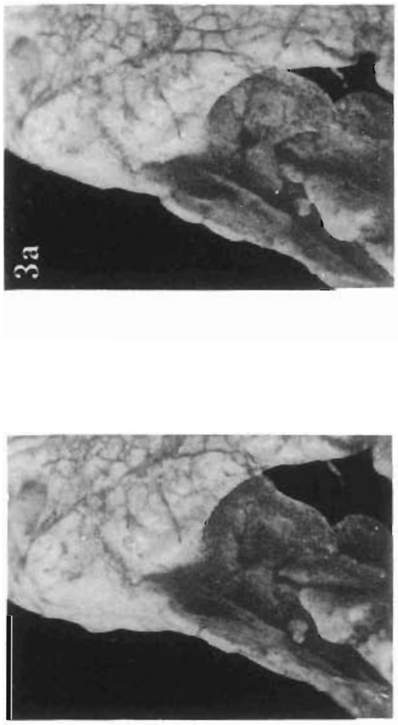
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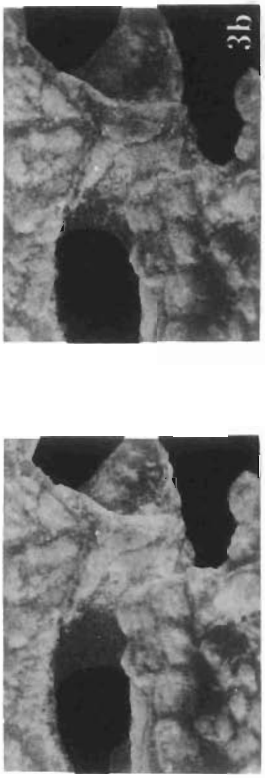
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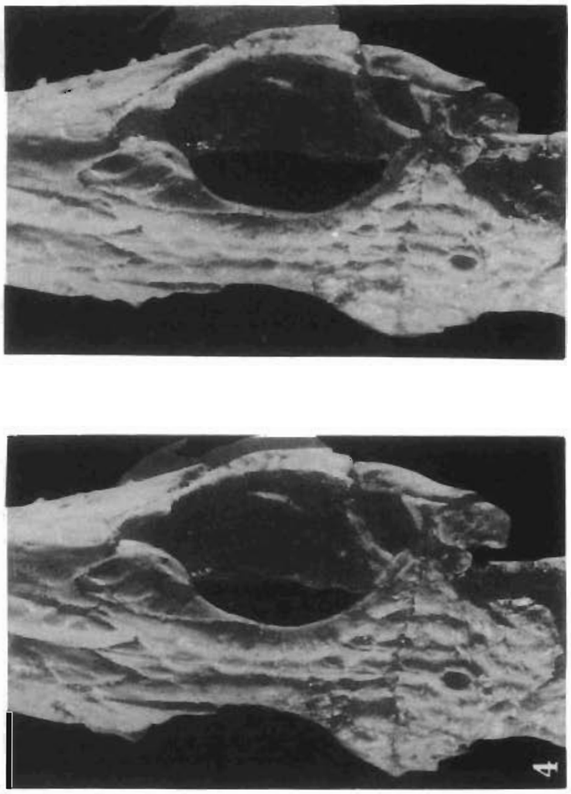
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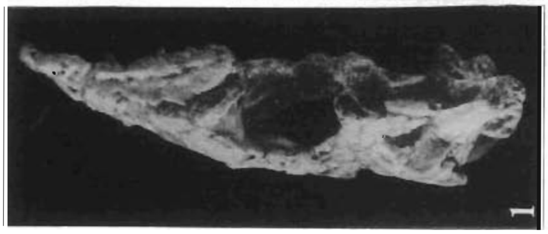
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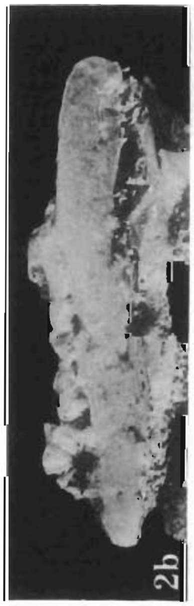
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