THE COMPARATIVE ANATOMY AND SYSTEMATICS OF MESOZOIC SPHENODONTIDANS

XIAO-CHUN WU

BIOLOGY DEPARTMENT

McGILL UNIVERSITY, MONTREAL

QUEBEC, CANADA

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PREFACE

This thesis is centred around an anatomical study of the cranial osteology of the Mesozoic sphenodontidans, *Asiacephalosaurus wangi*, *Rarojugalosaurus mcgilli*, *Dianosaurus petilus* and *Homoeosaurus maximiliani*. The first two are newly discovered and have not been studied previously. The third, previously described only in a preliminary fashion, was misinterpreted as a protorosaur. Although many specimens of *H. maximiliani* have been described (Cocude-Michel, 1963; Faber, 1981) since the species was first named by Meyer (1845), the newly exposed dorsal part of the skull of a new specimen has provided many new cranial features. Consequently, it was necessary to examine, draw and describe all of these sphenodontidans. The descriptions are all original and present a virtually complete picture of the cranial osteology of these genera for the first time. In addition, the different patterns of the middle ear apparatus of the Sphenodontida and the functional problems of the temporal region in the Lepidosauria have been considered. Although use is made of the literature to obtain background data, the conclusions drawn are original unless explicitly stated otherwise. Finally, the detailed descriptions of the four genera have permitted a reassessment of the phylogeny of the Sphenodontida. After reviewing the literature, original conclusions are given.

ACKNOWLEDGEMENTS

This study owns its existence to the supervision of Dr. Robert L. Carroll who critically read and edited several drafts of this manuscript, and I am greatly indebted for his interest and encouragement. I would like to express my appreciation to the other members of my dissertation committee--Drs. Joan Marsdon, Robert E. Lemon, and David M. Green--for their time, effort and patience, and especially to Dr. D. M. Green for his comments and help in obtaining a preserved specimen of the living Sphenodon punctatus. I am very grateful to Dr. Robert Holmes for his proofreading the manuscript and improving it considerably. I am also grateful to professor Ai-lin Sun (Institute of Vertebrate Paleontology and Palaeoanthropology, Academia Sinica, Beijing, China) and Dr. Sankar Chatterjee (The Museum of Texas Tech University, Lubbock, Texas) for their suggestions and encouragements.

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I have particularly benefitted from Mr. K. Lin's and Dr.

D. M. Green's knowledge of Mix Parsimonious Algorithm in PHYLIP Package and other computer programs. I thank Dr. Pierre-Yves Gagnier for his help translating the French version of the abstract. My thanks are also due to Mrs. Pamela Gaskill for her initial guidance in drafting the figures and encouragement, Dr. David Berman (Carnegie Museum, Pittsburgh) for permit to study the material of Homoeosaurus maximiliani, Dr. C. H. Daugherty (the School of Biological Sciences, Victoria University, Wellington, New Zealand) for providing a preserved specimen of the living Sphenodon punctatus (from Stephen Island), Mr. F. L. Li (The Kunming Branch of Chinese Academy of Sciences, Kunming, Yunnan, China) for providing preserved specimens of Japalura laviceps (from Sichuan province), Mrs. Messrs R. Lamarche and G. L'heureux for photographic work, Mrs. Z. J. Wang, H. Wang (The Culture Museum of Lufeng County, Yunnan, China) and F. Yi (Dawa Elementary School, Lufeng, China) for their help during my field work. In addition, I have received considerable assistance from the staff, especially from Ingrid Birker and Marie La Ricca, at the Redpath Museum. Finally, I would like to thank my wife, Wen-ying Lu, for her encouragement and support throughout the preparation of this thesis.

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ABSTRACT

Two new sphenodontidans, *Asiacephalosaurus wangi* gen. et sp. nov. and *Rarojugalosaurus mcgilli* gen. et sp. nov., from the Early Jurassic of China are described. The sphenodontidan status of *Dianosaurus petilus* Young 1982 from the Late Triassic of China is determined. Based on a new specimen of *Homoeosaurus maximiliani* Meyer 1845 from the Late Jurassic of Germany, cranial features unique within the Sphenodontida are established. Evidence from the braincase of fossil sphenodontidans demonstrates that an impedance matching middle ear is probably a synapomorphy of the Lepidosauria. Three patterns of the middle ear apparatus are examined in the Sphenodontida. The middle ear apparatus of the living *Sphenodon* has secondarily lost its impedance matching ability. The study of adductor jaw musculature suggests that the streptostyly of the quadrate is a derived state in the Lepidosauria, the retention of a fixed quadrate in early sphenodontidans with an incomplete lower temporal bar may have been required for precise tooth occlusion, and a solid lower temporal bar in later sphenodontidans may have served as a brace to support the lateral side of the quadrate condyle and thus prevents it from twisting anteriorly rather than posteriorly. It is hypothesized that a common ancestor shared by the Sphenodontida and the Squamata had a skull with an incomplete lower temporal bar but a rigid quadrate and that the dichotomy of the Sphenodontida and the Squamata must have

occurred before the origin of a streptostylic quadrate. Based on the broad palatine and anteriorly positioned parietal foramen, *Homoeosaurus* is more derived than all the Late Triassic-Early Jurassic genera. *Brachyrhinodon*, *Polysphenodon*, *Clevosaurus*, *Asiacephalosaurus*, *Rarojugalosaurus* and *Dianosaurus* can be informally referred to a monophyletic subgroup--the clevosaurs--which share a very weak or absent premaxillary process of the maxilla and a relatively short snout.

RÉSUMÉ

Deux nouvelles espèces, *Asiacephalosaurus wangi n.g.*, *n.sp*. et *Rarojugalosaurus megilli n.g.*, *n.sp*., sont décrites du Jurassique inférieur de Chine. *Dianosaurus petilus* Young 1982, du Trias supérieur de Chine est attribué aux Sphénodontides.

Un nouveau spécimen d'*Homoeosaurus maximiliani* Meyer 1845 du Jurassique supérieur d'Allemagne montre des caractères crâniaux uniques chez les Sphénodontides. Le foramen pariétal en position antérieur et le large palet suggèrent qu'*Homoeosaurus* est plus dérivé que tous les autres genres du Trias terminal-Jurassique inférieur. Les genres *Brachyrhinodon*, *Polysphenodon*, *Clevosaurus*, *Asiacephalosaurus*, *Rarojugalosaurus* et *Dianosaurus* peuvent être attribués de façon informelle au sous-groupe monophylétique des Clévosaures, parmi les Sphénodontides. Les Clévosaures partagent un processus prémaxillaire réduit ou absent et un museau très court.

Trois dispositions de l'oreille moyenne sont observées chez les Sphénodontides: une oreille moyenne de type Lézard, un cadre tympanique renversé, et une oreille moyenne réduite. L'oreille moyenne du Sphenodon actuel n'a pas la capacité **de faire concorder l'impédance**, alors que la structure du crâne des Sphénodontides fossiles démontre que l'oreille moyenne possédait cette capacité. Ce caractère représente une synapomorphie des Lépidosauriens.

L'étude de la musculature adductrice de la mâchoire

suggère que la streptostylie du carré est un caractère dérivé pour les Lépidosauriens. La rétention d'un carré fixe et d'une barre temporale inférieure incomplète pourrait être requise pour l'occlusion dentaire chez les premiers représentants des Sphénodontides. Une barre temporale inférieure solide chez les représentants plus tardifs des Sphénodontides servirait d'ancrage pour maintenir le coté latéral du condyle du carré afin de prévenir un balancement antérieur au lieu de postérieur.

Il est suggéré qu'un ancêtre commun aux Squamates et Sphénodontides partageait un crâne avec une barre temporale inférieure incomplète mais un carré rigide. La divergence entre Squamates et Sphénodontes a du s'établire avant l'origine d'un carré streptostylique.

INTRODUCTION

In contrast with other modern reptile groups, sphenodontidans only have a single living genus and two species, Sphenodon punctatus Gray and S. guentheri (Daugherty et al., 1990), generally both called the Tuatara. These two species survive on a few isolated islands off the New Zealand coast and have no fossil record. However, the sphenodontidans as a group were common and widespread during a period from about 100 million years to 200 million years ago. Their fossil remains have been found in Europe, North America, southern Africa and Asia.

The sphenodontidans have been considered to be close relatives of the Triassic rhynchosaurs since the suggestion was first made by Owen in 1845 and Huxley in 1869 (see Carroll, 1985). Both groups were grouped together within the diapsid order Rhynchocephalia in the subclass Lepidosauria (Romer, 1966). Recent work has questioned the affinities of the extinct rhynchosaurs and the sphenodontidans. The supposed acrodont teeth of the rhynchosaurs are clearly set in deep sockets (Chatterjee, 1974; Benton, 1983), and the ankle joint is similar to that of primitive archosaurs (Carroll, 1976; Thulborn, 1980; Brinkman, 1981). Recently, a number of authors (Benton, 1983, 1984 and 1985; Brinkman, 1981; Carroll, 1976, 1985, and 1988a; Evans, 1984, 1986 and 1988; Gaffney, 1980; Gauthier, 1984; Gow, 1975; Hughes, 1963; Thulborn, 1980;) have suggested that the rhynchosaurs, prolacertiforms, and archosaurs form a natural assemblage, the Archosauromorpha (Huene, 1946), resurrected by Gauthier (1984). At the same time it has been shown that the sphenodontidans are more closely related to the Squamata (including lizards, snakes and amphisbaenians) than to the archosauromorphs (Carroll, 1977, 1985, 1988a and 1988b; Evens, 1984 and 1988; Benton, 1984 and 1985; Gauthier, 1984; Gauthier et al, 1988). The term Lepidosauria has been restricted to the squamates and the sphenodontidans within the Lepidosauromorpha (Gauthier, 1984).

Most workers have included *Sphenodon* and its fossil relatives in a single family, the Sphenodontidae (Cope, 1870), although some others have referred them to a suborder the Sphenodontia (Nopsca, 1923; Williston, 1925; Hoffstetter, 1955; Evans, 1984; Benton, 1985) or the Sphenodontoidea (Kuhn, 1969; Fraser, 1982; Whiteside, 1986). The name of the order Rhynchocephalia was erected to include the genus *Sphenodon* by Gunther in 1867, and the rhynchosaurs were added later. Now that it is judged necessary to separate the two groups, the name Rhynchocephalia might logically be retained for *Sphenodon* and its allies. However, Estes (1983) suggested that *Sphenodon* and all its fossil relatives be placed in a separate order, the Sphenodontida, in order to avoid the confusing similarity of the names of the order Rhynchocephalia and the rhynchosaurs. As with Carroll (1985), Fraser (1988) and Fraser and Benton (1989), I follow Estes in accepting the Sphenodontida as the ordinal name, and I consider the pleurosaurs (see Carroll, 1985) and *Gephyrosaurus* (Evans,

1980) as members of this order.

It has long been assumed that the living genus Sphenodon shows a more primitive anatomy than any other living diapsids. It is thought to have changed little over the past 200 million years and remains today relatively unchanged from Late Permian diapsids. For example, it has complete upper and lower temporal bars, it shows no tympanum or air-filled middle ear cavity and retains a sprawling posture accompanied by sinusoidal locomotion. Consequently, Sphenodon has been called a 'living fossil' in various text-books (e.g. Goin et al., 1978).

However, this assumption has been challenged by the studies of the early sphenodontidans in recent years. In 1985 Carroll pointed out that the presence of an incomplete lower temporal bar in some early members raised the possibility that the solid lower temporal bar of Sphenodon might have evolved within the group. Later, Whiteside (1986) demonstrated that the sutural pattern of the lower temporal bar was not homologous between Sphenodon and primitive diapsids, which implies a secondary acquisition of the lower temporal bar of Sphenodon. In addition, other authors (Robinson, 1973; Gans and Wever, 1976; Weaver, 1978; Whiteside, 1986; etc.) believe that the auditory apparatus of Sphenodon shows a degenerate condition but there is little direct evidence from the braincase of the fossil species to refute the traditional idea that the middle ear of Sphenodon retains a primitive pattern inherited from early diapsids.

The early evolution of the Sphenodontida is not well documented in the fossil record. Hence the origin and phylogenetic relationships of member genera have been subject to debate. Since the 1970's, more than six new genera of sphenodontidans has been described from the Upper Triassic--Lower Jurassic fissure fillings of England (Evans, 1980 and 1981; Fraser, 1982 and 1986; Whiteside, 1986) and several earlier known fossils have been restudied (Robinson, 1973; Carroll, 1985; Fraser, 1988; Fraser and Benton, 1989). Undoubtedly, these findings and restudies are very important to our knowledge of the morphology and history of the early sphenodontidans, but unfortunately, none of the fossils so far known have well-preserved braincase material and most of them are based on isolated bones or very fragmentary specimens.

The first Late Triassic-Early Jurassic material from Asia that could be assigned confidently to the Sphenodontida was Dianosaurus petilus Young, 1982. It was recovered from the Lower Lufeng Formation of the Lufeng Basin, Yunnan province, Southwest China. As with the majority of other small tetrapod fossils of the formation, the specimen is preserved in a nodule. It was not adequately prepared prior to the initial description. As a result, it was initially thought to be a protorosaurian. Three additional skulls of two previously unrecognized sphenodontidan genera, Asiacephalosaurus and Rarojugalosaurus, were collected by the author from the Lower Lufeng Formation of the same basin in 1984. Together with Dianosaurus petilus, this material comprises the major part of this thesis.

In addition, a skeleton of the Upper Jurassic genus Homoeosaurus from Europe will be also described for comparative purposes. No fossil sphenodontidans have been found from deposits of middle Jurassic or post-late Cretaceous sediments. Hence, the Late Jurassic Homoeosaurus provide an important temporal intermediate between the early Mesozoic genera and the living Sphenodon. Homoeosaurus was established by Meyer in 1845. Since then, a great many specimens of this genus have been collected from the Solnhofen Limestone and deposits of equivalent age in Europe, but the skull morphology is still not well understood. This is due partially to the peculiar preservation of the specimens and partially to the fact that no one has so far made serious efforts to prepare the skull from the reverse side of the exposed slabs.

In addition to describing the cranial anatomy of the four taxa, I will discuss the auditory evolution of the Sphenodontida by comparing the morphology of the middle ear region of the fossil genera with that of modern lizards. I will also examine whether a fixed or a streptostylic quadrate represents a primitive status in the Lepidosauria and its significance to feeding mechanism through a functional analysis of the head musculature of selected lizards and Sphenodon. With new information from this study, I will establish group relationships within the Sphenodontida by making use of the procedures of cladistic analysis (Hennig, 1966; Eldredge and Cracraft, 1980; Wiley, 1981; etc.).

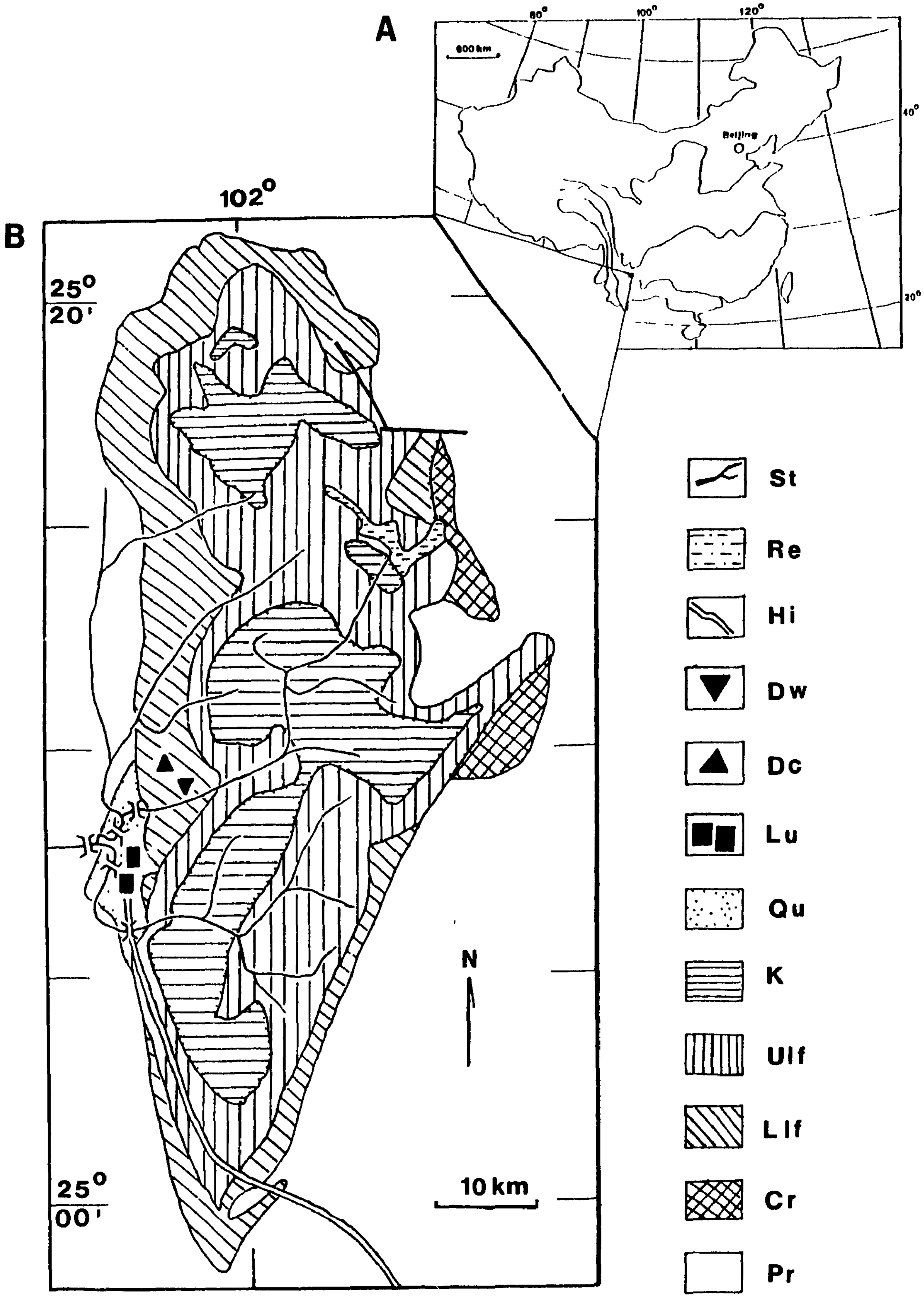
MATERIALS AND METHODS

As early as 1941, the sediments of the Lufeng Basin were demonstrated to hold a richly varied vertebrate fauna (Bien, 1941). In a series of early papers, Young (1939-1948) described the vertebrate assemblage, later naming it the Lufeng Saurischian Fauna in a monographic paper (1951). Since then, many new taxa have been added to the fauna (Sun et al., 1985). Three sphenodontidan genera studied here represent some of the latest additions.

The Lufeng Basin is of small size, with a length approximately one hundred km from north to south and an average width about thirty km from east to west. It is situated in Lufeng county, about fifty-five km northwest of Kunming, the capital city of Yunnan province. Figure 1 presents the general stratigraphic relationships of the sediments of the Lufeng Basin.

The fossil remains are confined to the Lower Lufeng Formation (see Sun et al., 1985) or Series (Bien, 1941; Young, 1951; Simmons, 1965). Lithologically, the formation consists of alternating beds of dull purplish and dark red mudstone and sandy mudstone interbedded with thin sandstones. The geological age of the Lufeng Saurischian Fauna has been a subject of debate for years. Young argued that it was of Rhaetic age, while others suggest it to be of Liassic, or Rhaetic-Liassic for various reasons (see Sun et al., 1985). Most recent work on small diapsids (Sun et al., 1985; Wu,

Fig. 1. A, map of China; B, geological map of the Lufeng basin. Cr--Cambrian rock, Dc--Dachong village, Dw--Dawa village, Hi--Highway to Kunming, K--Cretaceous rock, Llf--Lower Lufeng Formation, Lu--Lufeng prefecture, Pr--Proterozoic rock, Qu--Quaternary deposit, Re--Reservoir, St--Stream, Ulf--Upper Lufeng Formation.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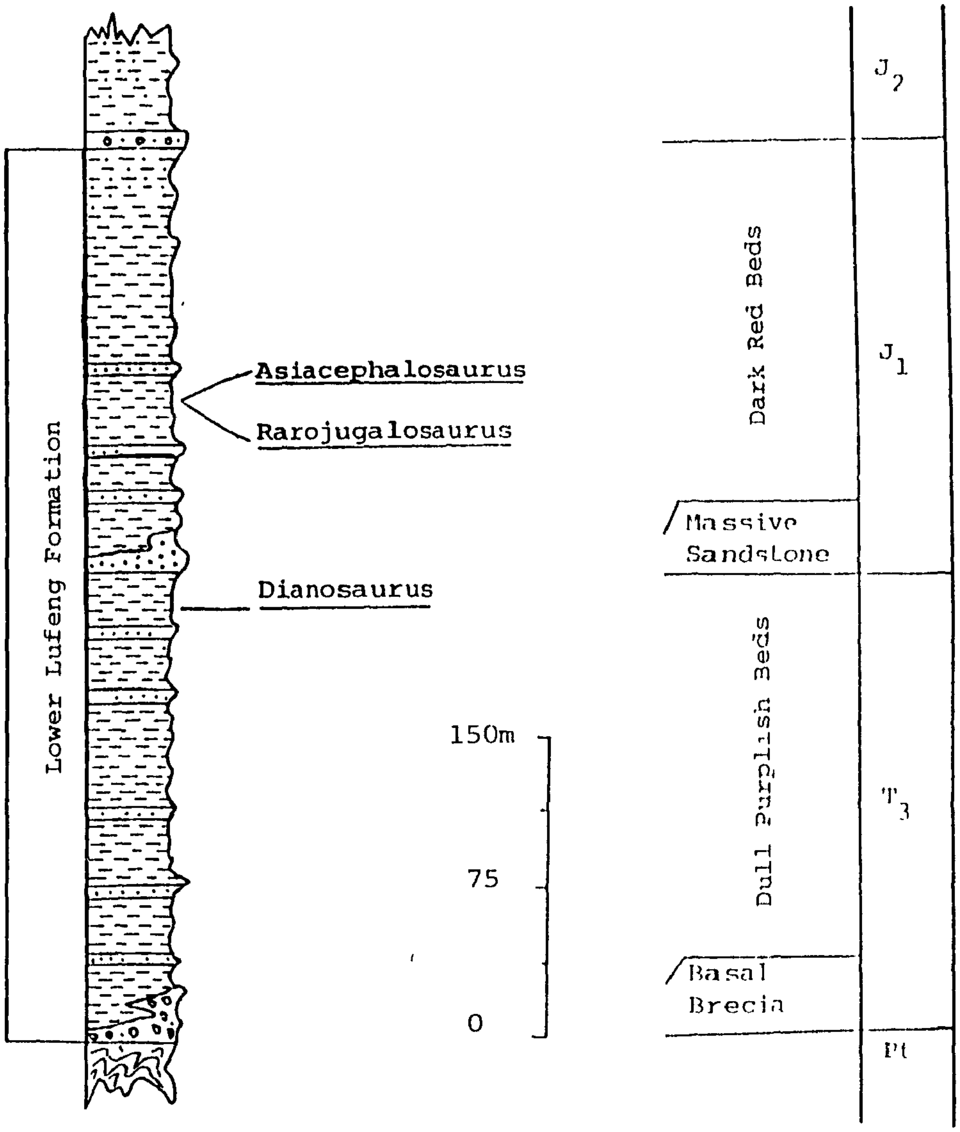
1986) suggests that two vertebrate assemblages can be established within the Lower Lufeng Formation. The lower assemblage from the lower part of the Lower Lufeng Formation (commonly called the Dull Purplish Beds), dominated by saurischian dinosaurs and *Bienotherium* tritylodonts, is of the Late Triassic age (Fig. 2). The upper assemblage from the upper part of the Lower Lufeng Formation (generally called the Dark Red Beds) is characterized by the addition of certain advanced groups: ornithischian dinosaurs, crocodylomorphs and mammals. It is considered to be of Early Jurassic age. The sphenodontidans in the Lufeng Basin appeared in both assemblages. *Dianosaurus* is found in the top of the Dull Purplish Beds, while *Asiacephalosaurus* and *Rarojugalosaurus* are from the middle of the Dark red Beds.

The specimens of *Dianosaurus* (V.4007) and two new genera (V.8271, V.8272, and V.8273) belong to the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), *Academia Sinica* (Chinese Academy of Sciences), in Beijing, China. The specimen of *Homoeosaurus* (C.M.6438) was loaned to the Redpath Museum, McGill University in Montreal by the Carnegie Museum in Pittsburgh. The preparations of all the specimens were undertaken by the author, primarily using dental drills, a Chicago Pneumatic Scribe (air driven reciprocal chisel) and mounted needles, under a binocular dissecting microscope.

The Chinese specimens are preserved in ferruginous nodules that are very hard. Before mechanical preparation was attempted, rough preparation was made by using more than 40%

Fig. 2. Sphenodontidan-bearing beds in Lower Lufeng Formation.


Lower Lufeng Formation
Asiacephalosaurus
Rarojugalosaurus
Dianosaurus
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Dark Red Beds
Massive Sandstone
Dull Purplish Beds
Basal Brecia
J_2
J_1
T_3
Pt

acetic acid. The author dipped fine sable hair brushes in the acid to brush the working areas and then washed the areas after each brushing. The acid treatment continued until bone was exposed. This technique works very well if employed with great care.

The major preparation of the specimen of Homoeosaurus was done on the hidden dorsal side of the head region. The skull roof was carefully exposed by making a "window" from the back of the specimen. Acid treatment was not used in spite of the calcareous nature of its matrix because of crystallization of calcite in bone.

Asiacephalosaurus wangi

Systematic Paleontology

Asiacephalosaurus, gen. nov.

Type Species--Asiacephalosaurus wangi, gen. et sp. nov.

Etymology--Asia referring to the continent from which the specimen has been collected. Cephalo from Greek Kephale (head), Saurus from Greek Sauros (lizard).

Diagnosis--A sphenodontidan differing from all others in having the following features: the paroccipital process fits into a fossa on the undersurface of the squamosal and separates the supratemporal from the cephalic head of the quadrate; the squamosal rests in a deep depression on the cephalic head of the quadrate; the supratemporal underlies the posteromedial margin of the squamosal; the dorsal process of the jugal slopes backwards to overlap the squamosal at a point beyond the midpoint of the supratemporal bar; the epipterygoid is expanded dorsally but narrow ventrally; the posterior process of the dentary tapers abruptly near the jaw articulation. This genus shares with Clevosaurus and Rarojugalosaurus a posterodorsal process of the premaxilla which excludes the maxilla from the external naris. It shares with Clevosaurus, Dianosaurus and Rarojugalosaurus a suborbital fenestra enclosed by only the palatine and ectopterygoid. It shares with Dianosaurus a depression on the rear part of the parabasisphenoid. It shares with Sphenodon and Palaeopleurosaurus an elongated central region of the pterygoid between the three rami.

Asiacephalosaurus wangi, sp. nov.

Holotype--V.8271: an almost complete but cracked skull with mandibles.

Locality--Near Dawa Village, Lufeng County, Yunnan Province, Southwest China.

Stratigraphic Position--Near the middle of the upper part (Dark Red Beds) of the Lower Lufeng Formation (Layer 8 in Table 4, see Sun et al., 1985).

Age--Probably Early Jurassic.

Etymology--In honour of Mr. Zheng-ju Wang for his contribution to the local vertebrate paleontology and palaeoanthropology during the past 30 years.

Diagnosis--As for genus.

Description

The skull was laterally compressed during fossilization. The left side posterior to the orbit is almost complete, but distorted. The left mandible is articulated with the skull. The tip of the rostrum, right side of the skull, and the right mandible are damaged. Palatal elements are present but incomplete. Although it was crushed to the left, the braincase is generally well-preserved.

a. General features of the skull (Figs. 3--6)

The skull is approximately 3 cm long. It is similar in configuration to that of Clevosaurus (Fraser, 1988). In dorsal view, the maxilla does not enter the margin of the external naris. The suborbital fenestra is banana-shaped and enclosed by only the palatine and ectopterygoid. The nasals, frontals and probably the parietals are paired. The supratemporal is retained. The lacrimal is absent. The lower temporal bar extends laterally beyond the primitive limits of the adductor chamber.

Although the inferior temporal fenestra is comparable to the orbit in size, the oval supratemporal fenestra is much smaller. In Clevosaurus the three openings are almost of the same size.

In lateral view, the mandible shows a pronounced coronoid process posterior to the dentition and probably has a prominent retroarticular process posteriorly based on broken surface. The maxilla is deep dorsoventrally with an obtuse posterior termination. The beak-like structure of the snout is restored on the basis of that of Clevosaurus and Rarojugalosaurus.

In ventral view, the lateral row of palatine teeth parallels the maxillary dentition anteriorly but gradually curves towards the midline posteriorly as in most early

Fig. 3. *Asiacephalosaurus wangi*, gen. et sp. nov.

Reconstruction of the skull in dorsal view.

Scale bar 5.0 mm.

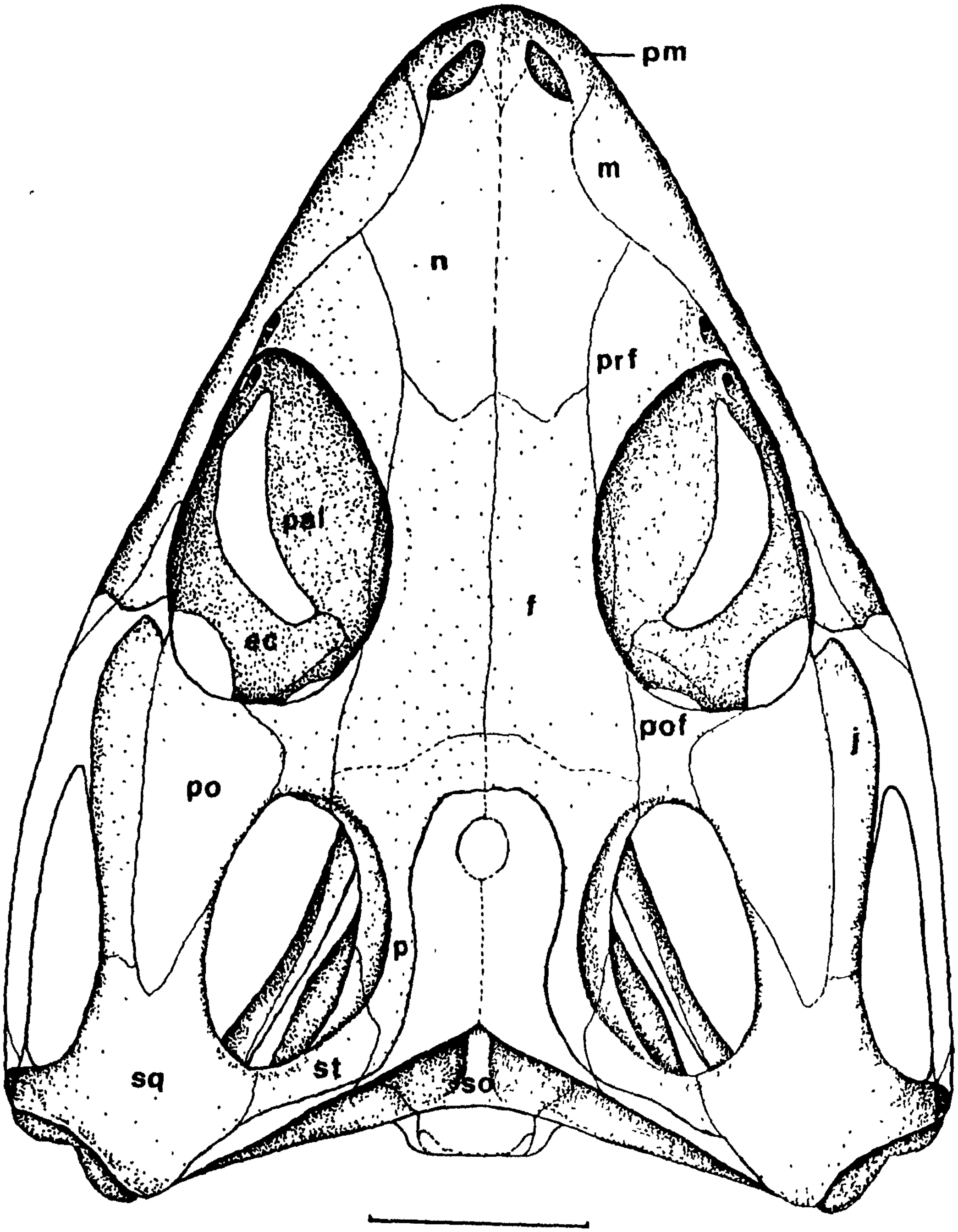
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Fig. 4. *Asiacephalosaurus wangi*, gen. et sp. nov. Reconstruction of the skull in lateral view. Scale bar 5.0 mm.

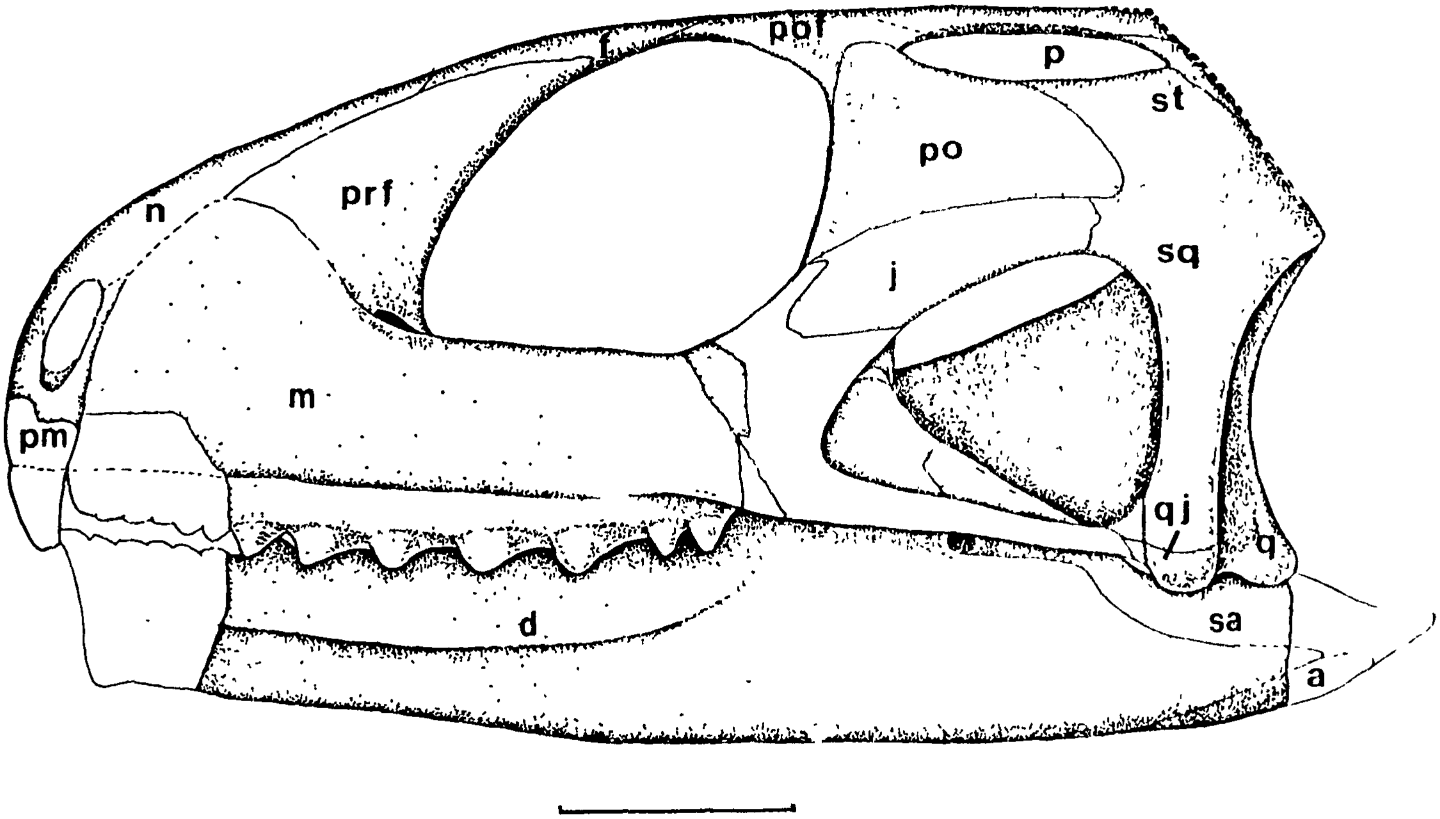

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Fig. 5. *Asiacephalosaurus wangi*, gen. et sp. nov. Reconstruction of the skull in ventral view. Scale bar 5.0 mm.

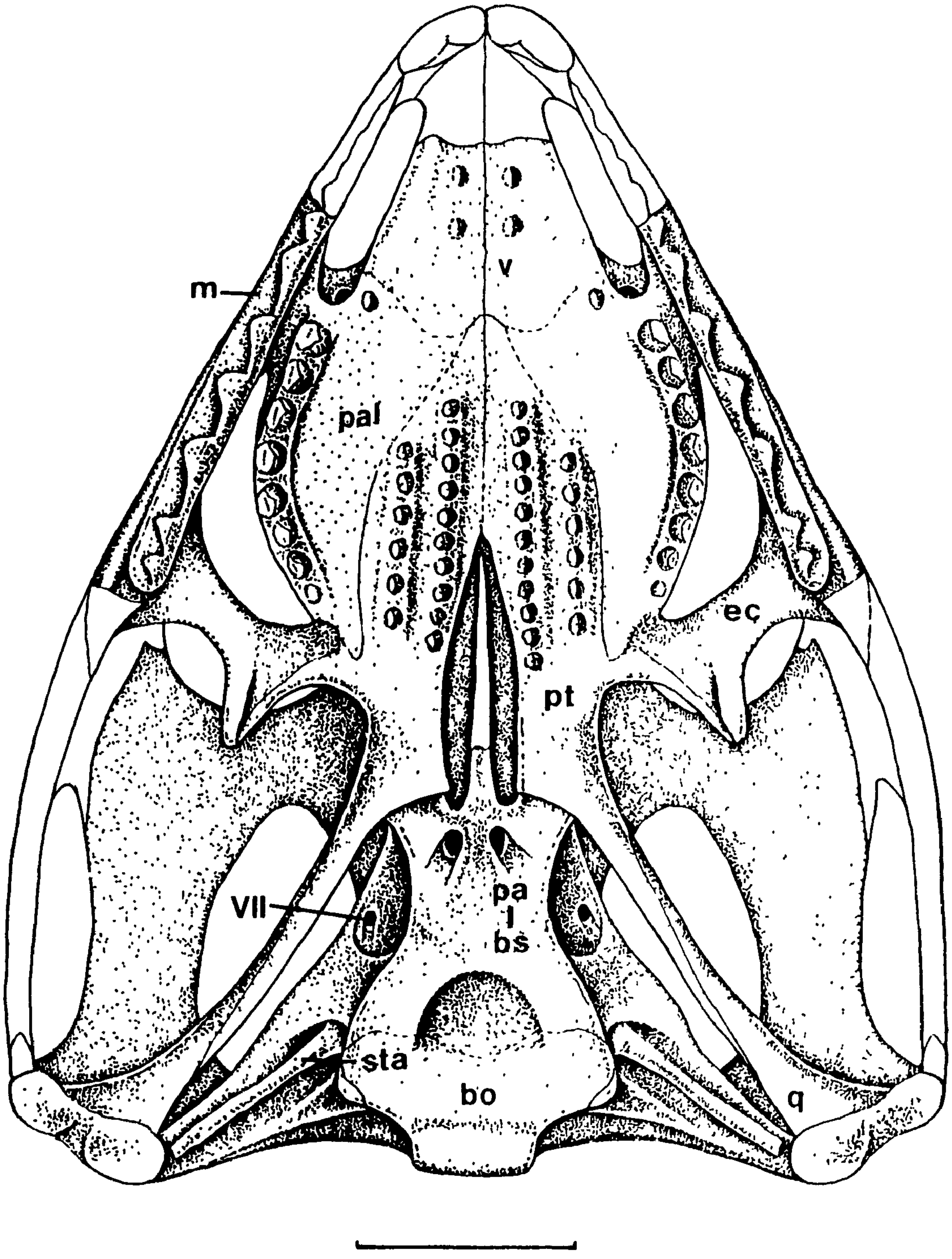
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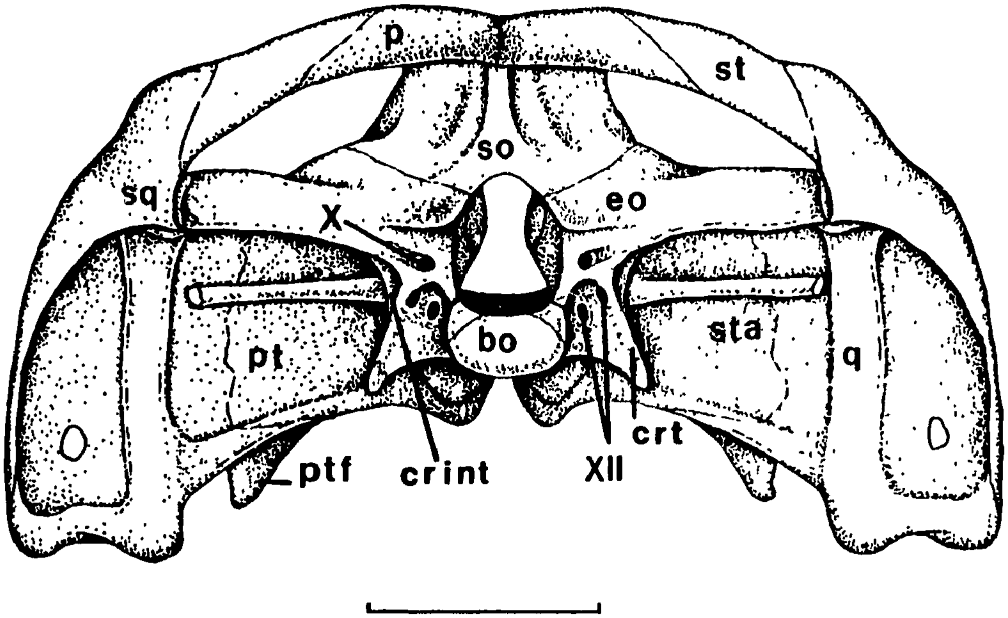
Fig. 6. Asiacephalosaurus wangi, gen. et sp. nov. Reconstruction of the skull in occipital view. Scale bar 5.0 mm.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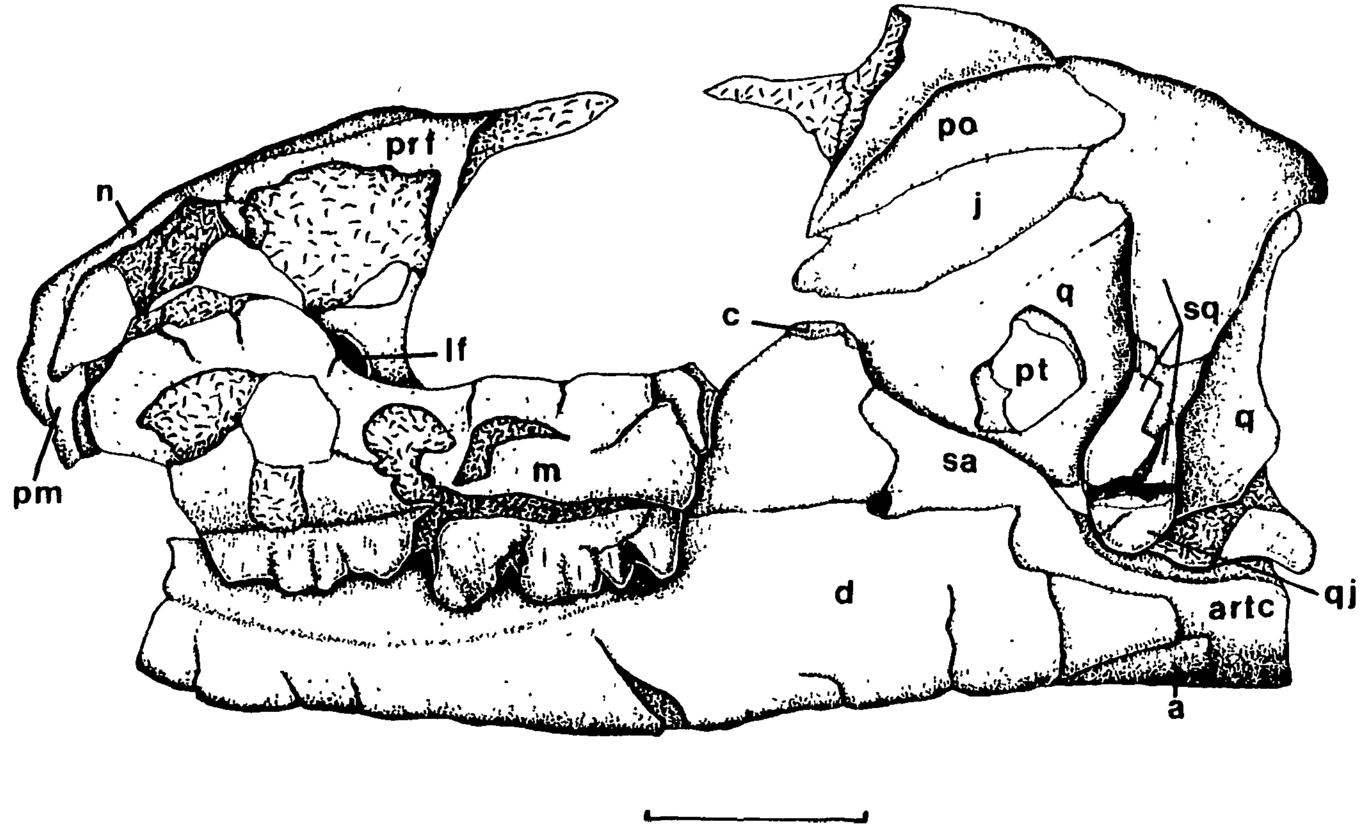
sphenodontidans. There are two rows of pterygoid teeth. The pterygoid does not enter the suborbital fenestra as in *Sphenodon* and most fossil species. There is a semicircular depression on the ventral surface of the parabasisphenoid that probably reaches the basioccipital posteriorly.

In contrast to that of *Sphenodon* and *Clevosaurus*, the middle ear region of the braincase is very similar in structure to that of modern lizards: the middle ear cavity is well-developed, the occipital recess is present on the basal tubercle, the fenestra rotundum is separated from the metotic fissure and the recess vena jugularis is evident on the anterolateral wall of the braincase although it is of limited extent. However, an unossified gap is present anteroventral to the ventral process of the opisthotic as described in *Sphenodon* and *Clevosaurus* (Fraser, 1988). Viewed posteriorly, the medial wall of the otic capsule is fully ossified. This is in contrast with a membranous condition in *Sphenodon*. The quadrate is much deeper than that of *Sphenodon*, reaching about 59% of the height of the skull. The post-temporal fenestra is small and the braincase is shallow.

b. Dermal bones of the skull roof (Figs 7--10)

The premaxillae are badly damaged, but appear to be similar to those of *Clevosaurus*. The left premaxilla bears a posterodorsal process that separates the maxilla from the external naris as described in *Clevosaurus*. The posterior

Fig. 7. <u>Asiacephalosaurus</u> <u>wangi</u>, gen. et sp. nov. Lateral view of the skull. Scale bar 5.0 mm.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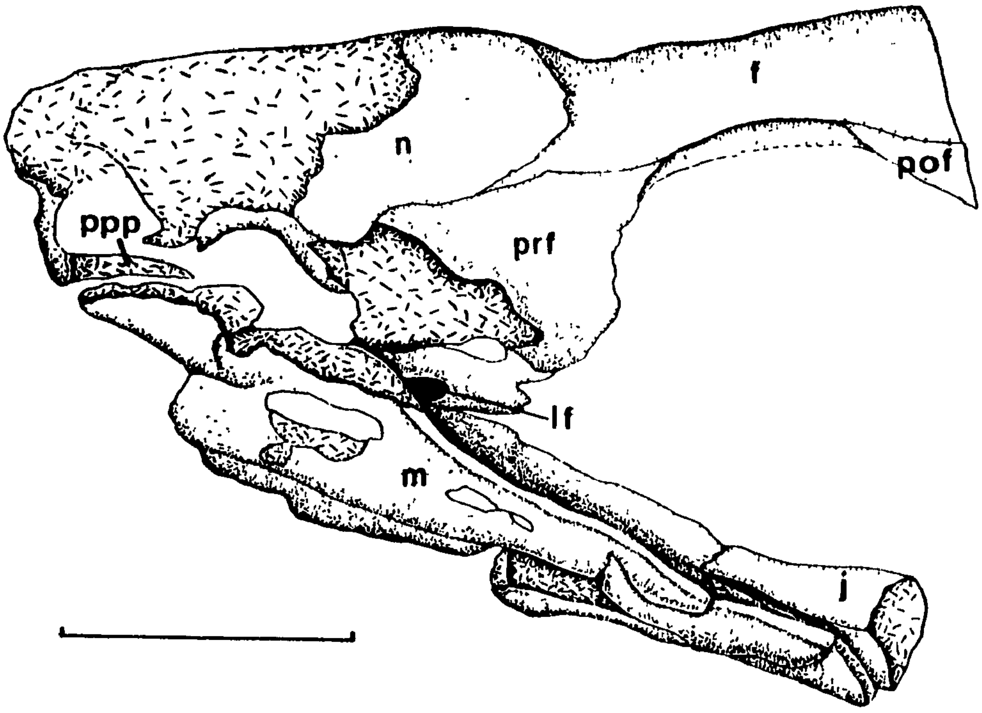
process is overlapped by the maxilla.

The left maxilla is almost complete. Its anterodorsal process extensively overlaps the premaxilla anteriorly, and the nasal and prefrontal dorsally. Ventromedial to the orbital margin the maxilla forms a shelf-like palatal process, which meets the prefrontal, palatine and ectopterygoid. Its palatal process disappears along the posterior half of the orbit margin where the maxilla sheathes the anterior process of the jugal. As in Sphenodon, the lateral aspect of the maxilla is concave above the marginal dentition. Although incomplete, its posterior process indicates that the maxilla bows posterolaterally posterior to the tooth row around the adductor chamber as in most sphenodontidans.

The nasals have been eroded on both sides except for parts near their suture with the frontals. Nevertheless, their configuration can be reconstructed from impressions. They are slightly different from those of Clevosaurus in having a combined W-shaped suture with the frontals. The nasal overlaps the frontal posteriorly. The damage of the bone obscures its relationship with the premaxilla. The opening of the external naris appears oval in shape and moderate in size.

The prefrontal is well-preserved on the left side although its surface was worn through in certain areas. As in most sphenodontidans, the bone is triangular in outline. It contributes to the anterodorsal edge of the orbit and has an extensive contact with the nasal and frontal. Its ventral process contacts the palatine at the anteroventral corner of

Fig. 8. Asiacephalosaurus wangi, gen. et sp. nov. Anterior part of the skull in laterodorsal view. Scale bar 5.0 mm.



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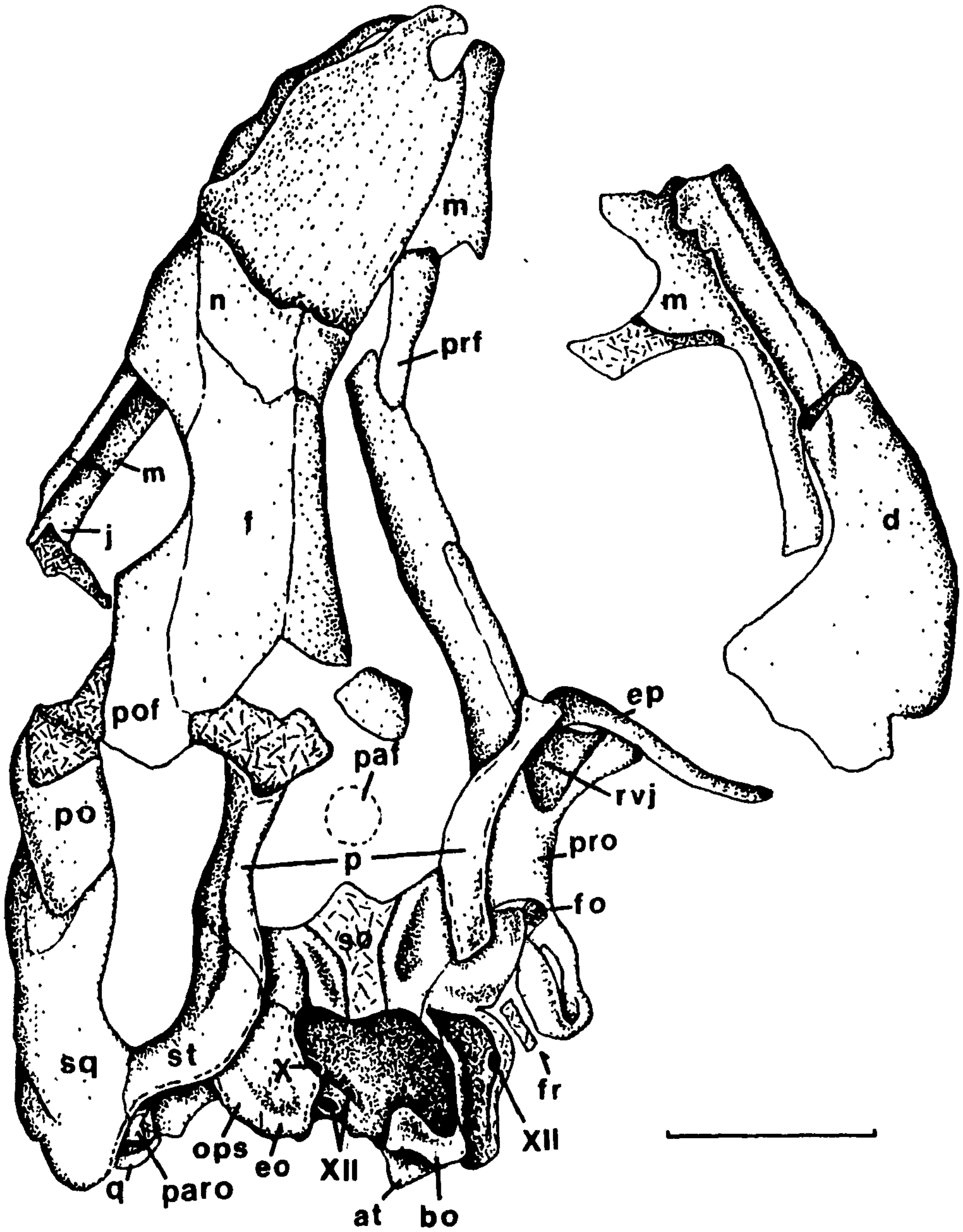
the orbit. Since there is no independent ossification of the lacrimal, the lacrimal foramen is laterally exposed and bounded ventrolaterally by the maxilla. In comparison with that of the known sphenodontidans, the prefrontal shows more surface exposure anterior to the orbit.

The frontals meet along the midline without complex interdigitation. The left frontal is complete except for the area articulating with the parietal. It is flat and broader posteriorly than anteriorly. Laterally, the bone enters the orbital margin for a relatively short distance. Its relationship with the postfrontal is clearly marked. The suture between the frontals and parietals may have been somewhat curved anteriorly.

The postfrontal is present on the left side. The element is normally a triradiate bone in diapsids, but here its ventral process and the area near the suture with the parietal are damaged. As in most sphenodontidans the postfrontal has an extensive contact with the lateral margin of the frontal and probably a short posterior process that overlaps the anterolateral edge of the parietal. It borders the orbit anteriorly and the supratemporal fenestra posteriorly.

The large, triangular postorbital is nearly complete on the left side, but is fractured by dorsoventral compression and damaged anteriorly. It widely overlaps the postfrontal dorsally and the anterior process of the squamosal, and surrounds the anterodorsal edge of the jugal extensively and contributes significantly to the supratemporal bar.

Fig. 9. *Asiacephalosaurus wangi*, gen. et sp. nov. Dorsal view of the skull. Scale bar 5.0 mm.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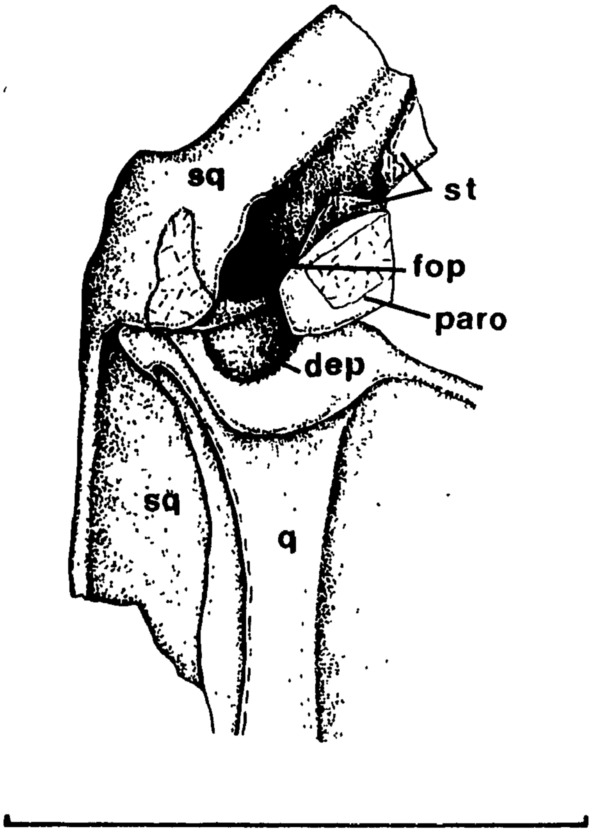
The jugal is represented by the anterior and dorsal processes on the left side. The two processes are widely separated because of the loss of the centre part from which the three processes usually radiate in diapsid reptiles. The anterior process is short and largely hidden in lateral view by the extensive overlap of the maxilla. On its ventral aspect a facet continuing to the maxilla probably receives the anterolateral process of the ectopterygoid as shown in Fig. 3. The dorsal process rigidly fixes the position of the postorbital dorsally and extends backwards over half of the length of the supratemporal bar to overlap the anterior process of the squamosal. As a result, the postorbital is excluded from the margin of the inferior temporal fenestra as is the case in the other fossil sphenodontidans. It is difficult to determine whether the posterior process of the jugal met the quadratojugal as in Clevosaurus or both the squamosal and the quadratojugal as in Sphenodon, or was free posteriorly as it is in some early sphenodontidans such as Diphydontosaurus (Whiteside, 1986) and Palaeopleurosaurus (Carroll, 1985), indicating an incomplete lower temporal bar (but see below).

The squamosal is well-preserved on the left side. The element is a large, more or less quadrilateral bone. Its anterior process forms the posterior part of the wide supratemporal bar, which was a common feature in the early sphenodontidans. Its descending process runs down along the lateral edge of the quadratojugal, contributing to the lateral rim of the tympanic crest to a point just above the condyle. Anteroventrally, the process is broken, which makes it impossible to obtain any direct evidence of its relationship with the jugal. It does not narrow towards its termination, suggesting that the squamosal may have made contact with the jugal at the posteroventral corner of the inferior temporal fenestra, as it does in some individuals of Planocephalosaurus (Fraser, 1982) and Sphenodon, forming a complete lower temporal bar. The descending process of the squamosal in Clevosaurus tapers ventrally, but it was thought that the process made weak contact with the jugal (Fraser, 1988). The posteromedial edge of the squamosal extensively overlaps the posterolateral extension of the supratemporal. This is in contrast with the case in Clevosaurus where the supratemporal overlaps the posteromedial margin of the squamosal. Near the posterodorsal tip of the squamosal, a deep fossa can be seen on the undersurface of the bone that obviously received the thickened lateral termination of the paroccipital process although the latter is a bit displaced. The squamosal fits ventrally into a basin-like depression on the cephalic head of the quadrate, forming a ball-and-socket articulation (Fig. 10).

The supratemporal is preserved on the left side. It is a strap-shaped bone positioned between the squamosal and the parietal. Medially, it extensively overlaps the posterolateral process of the parietal along the posteromedial margin of the supratemporal fenestra. A tiny bony fragment, tapered

Fig. 10. Asiacephalosaurus wangi, gen. et sp. nov. Relationships between the quadrate, the paroccipital process, the squamosal and the supratemporal. Scale bar 5.0 mm.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posteriorly and wedged between the paroccipital process and squamosal (Fig. 10), is most probably the distal end of the supratemporal. In contrast with Clevosaurus, the bone does not reach the cephalic head of the quadrate. This bone is absent in most other sphenodontidans.

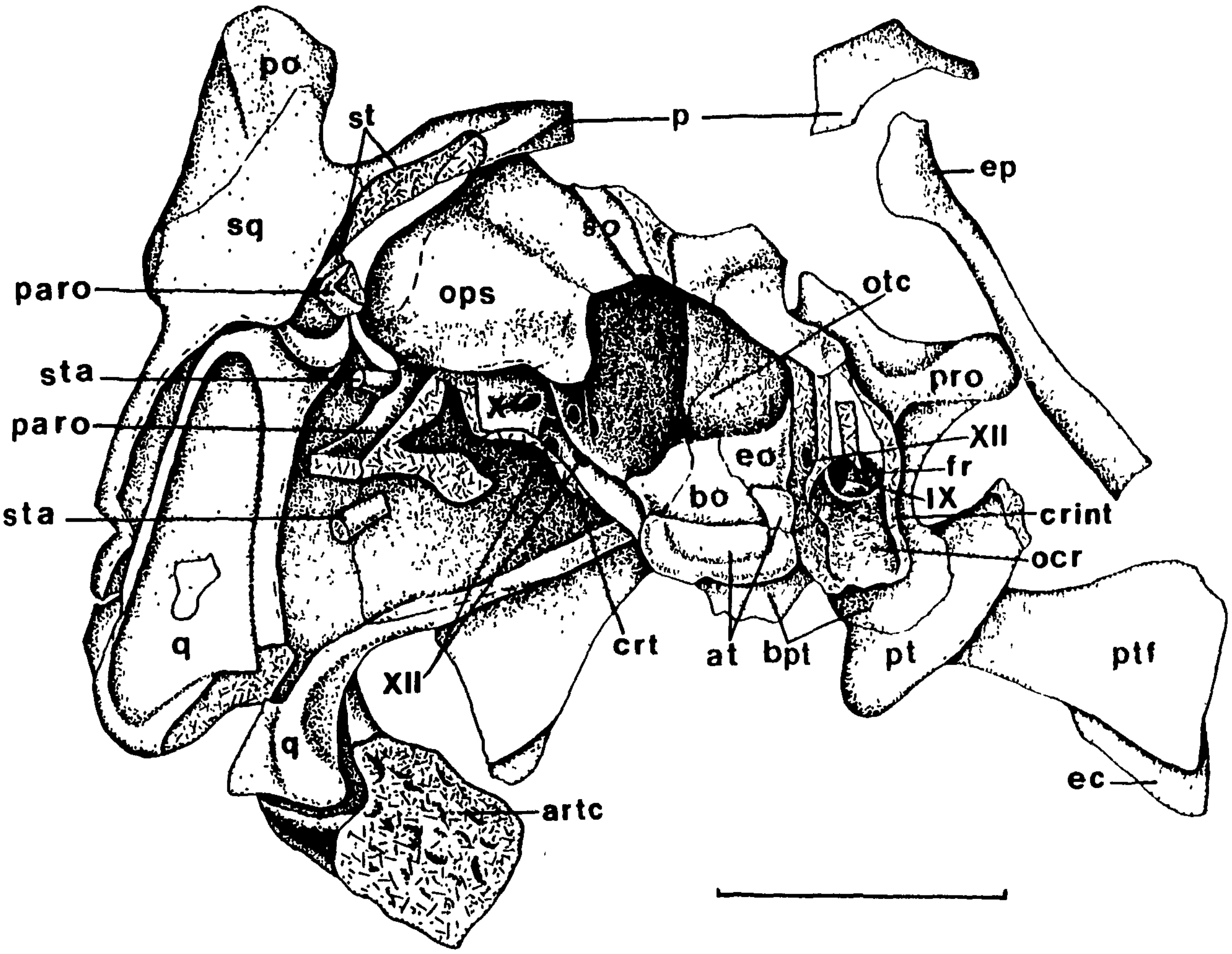
The parietals are not well-preserved on either side, but they are reconstructed as paired elements following the paired nature of the frontals. As the size of the supratemporal fenestra indicates, the bones are relatively larger in comparison to that of Clevosaurus and their width between the supratemporal passages is at least as broad as the interorbital region. As in Clevosaurus, each parietal slopes gently away from its lateral edge and forms the medial shelf of the supratemporal fenestra for the attachment of adductor muscles. Consequently, the parietal table is probably narrower than the interorbital width as in Gephyrosaurus (Evans, 1980) and Clevosaurus. The exact configuration of the parietal foramen is uncertain, but its anterior margin would not have reached the level between the anterior edges of the two supratemporal fenestrae.

The quadratojugal will be described with the quadrate since it is fused to the lateral surface of that bone.

c. **Palatoquadrate** (Figs 10, 11 and 7)

The quadrate complex is almost complete on the left side. The posterolateral surface of the complex forms a conch-like basin, bordered laterally by the tympanic crest, which is

Fig. 11. *Asiacephalosaurus wangi*, gen. et sp. nov. Occipital view of the skull. Scale bar 5.0 mm.



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strengthened by the overlap of the descending process of the squamosal, and medially by a posterior column that runs from the cephalic head of the quadrate down to the articulating surface for the lower jaw. The position of the quadratojugal can be established by the quadratojugal foramen in the basin, but no suture between it and the quadrate can be seen above or below the foramen. As in other sphenodontidans, the double condyle of the quadrate shows a large medial part and a small lateral surface. The broad pterygoid ramus is curved medially and expands anteromedially to overlap the quadrate ramus of the pterygoid, forming a deep, concave lateral wall of the middle ear cavity. With extensive contacts with both the squamosal and the pterygoid, the quadrate complex is tightly fixed to the skull. Because of poor preservation of its anteroventral surface, the relationship of the quadratojugal with the jugal remains uncertain.

The epipterygoid is well-preserved on the right side although it was somewhat twisted dorsally. The bone is very distinctive in having a shape that shows a reverse configuration of that of the epipterygoid of Sphenodon, i.e. an expanded dorsal end connected with the parietal and a narrow ventral tip that meets the pterygoid.

d. Dermal bones of the palate (Figs. 12 and 13)

The vomers can be recognized as paired triangular bones although they were damaged both anteriorly and posteriorly.

Fig. 12. *Asiacephalosaurus wangi*, gen. et sp. nov. Ventral view of the skull. Scale bar 5.0 mm.

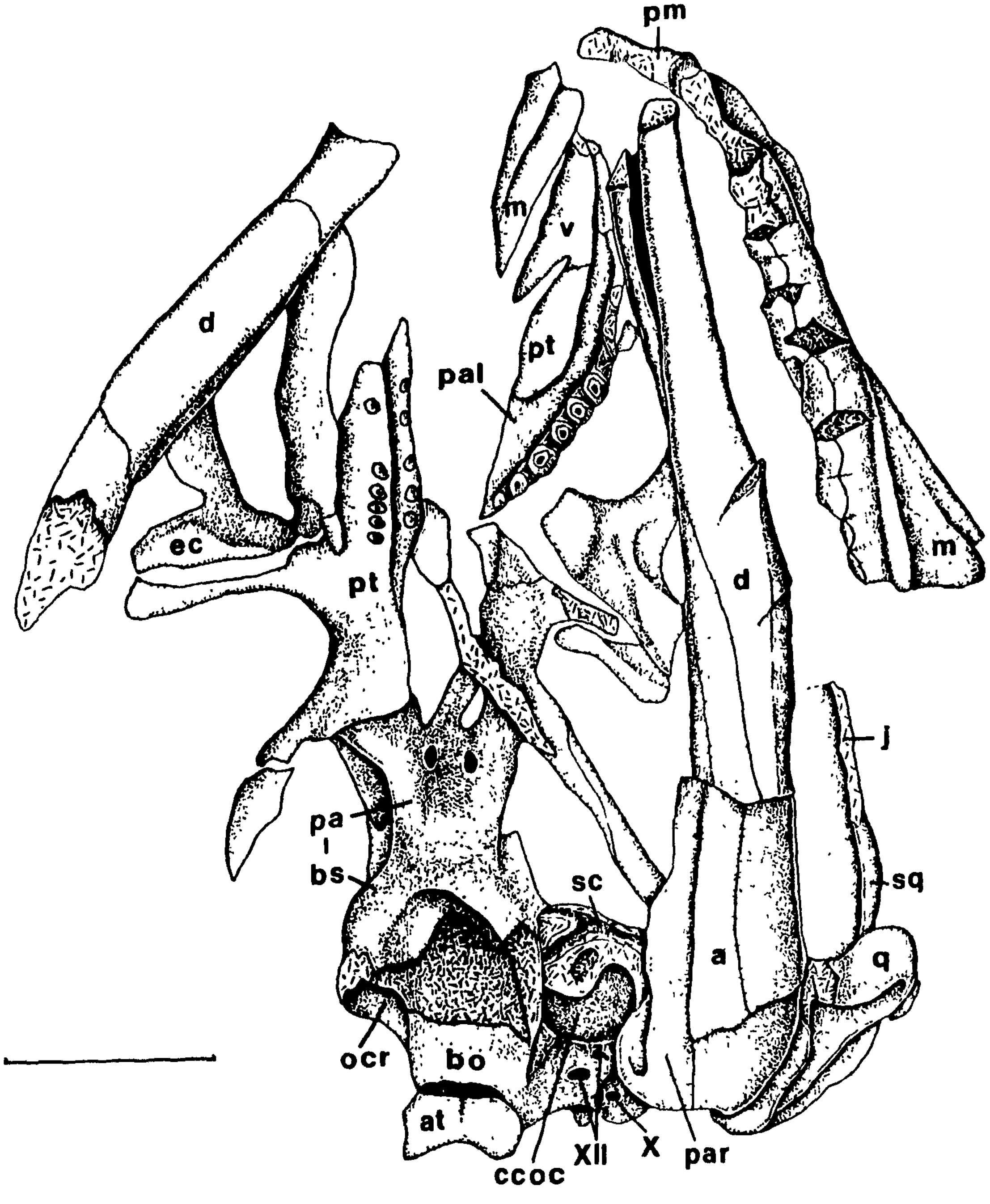
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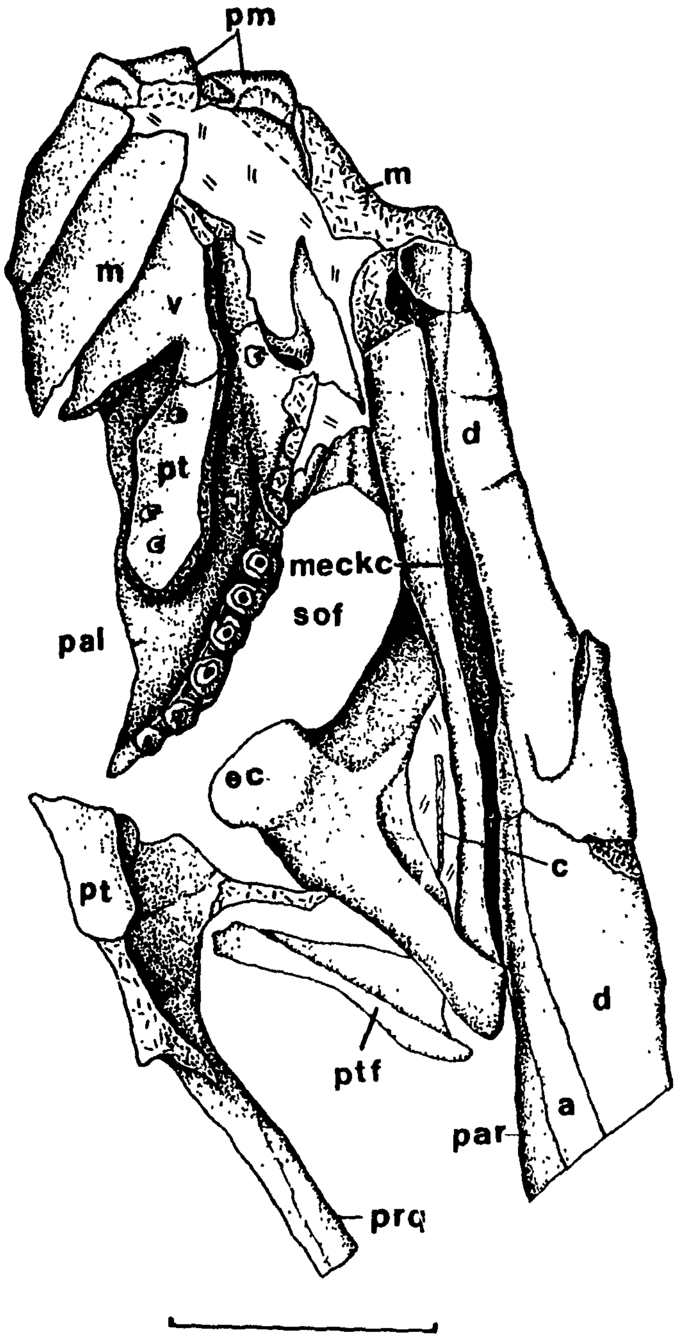
Fig. 13. Asiacephalosaurus wangi, gen. et sp. nov.
Anterior part of the skull in ventral view.
Scale bar 5.0 mm.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The bones contribute to the anterior part of the palate and border the choanae laterally. The suture between the vomers and the bones posterior to them was probably W-shaped. The right vomer is displaced over the left. The erosion has made it difficult to identify any more details.

The palatines are present on both sides and the left is almost complete. The maxillary process is a very robust shelf that slots into the maxilla laterally. The palatine encloses the choana anteriorly and slopes away from the anterior edge to form a posterior shelf to the nasal vacuity. On this shelf an opening is identified as the anterior exit of the infraorbital foramen that carries the superior alveolar nerve and artery into the anterior part of the maxilla. The body of the palatine has extensive contact with the pterygoid medially. It tapers posteriorly along the medial margin of the suborbital fenestra to wedge into the pterygoid. The enlarged lateral tooth row consists of approximately eight teeth that decrease in size posteriorly. In addition, a single palatine tooth lies anteromedial to the lateral row.

The pterygoids are relatively complete. Each can be divided into three rami that radiate from a central area and reach six other bones. The large, flat anterior ramus forms the lateral border of a moderate-sized interpterypoid vacuity, and with its counterpart passes anteriorly between the palatines. The transverse flange is deep and thickened distally. It extremely overlaps the ectopterygoid anteroventrally. The quadrate ramus is a large, fan-shaped lamina that is almost vertically orientated. The central area between the three rami is elongated as in Sphenodon and Palaeopleurosaurus. The pterygoid articulates firmly with the basipterygoid process.

The ectopterygoids are well-preserved on both sides, but are not entirely visible since the mandibles are still occluded. The element is robust and resembles the twisted H-shape described by Whiteside (1986) in Diphydontosaurus. In ventral view the medial bar of the H-shaped structure makes contact with the palatine anteriorly and forms the posterior border of the suborbital fenestra. From this region the bone extends posteroventrally into a tapering process that wraps around the anterolateral surface of the transverse flange of the pterygoid, forming a brace to guide jaw occlusion. The lateral bar slots into the jugal and maxilla laterally and runs forwards along the lateral border of the suborbital fenestra until it meets the maxillary process of the palatine anteriorly.

e. **Braincase** (Figs. 11, 12, 14 and 15)

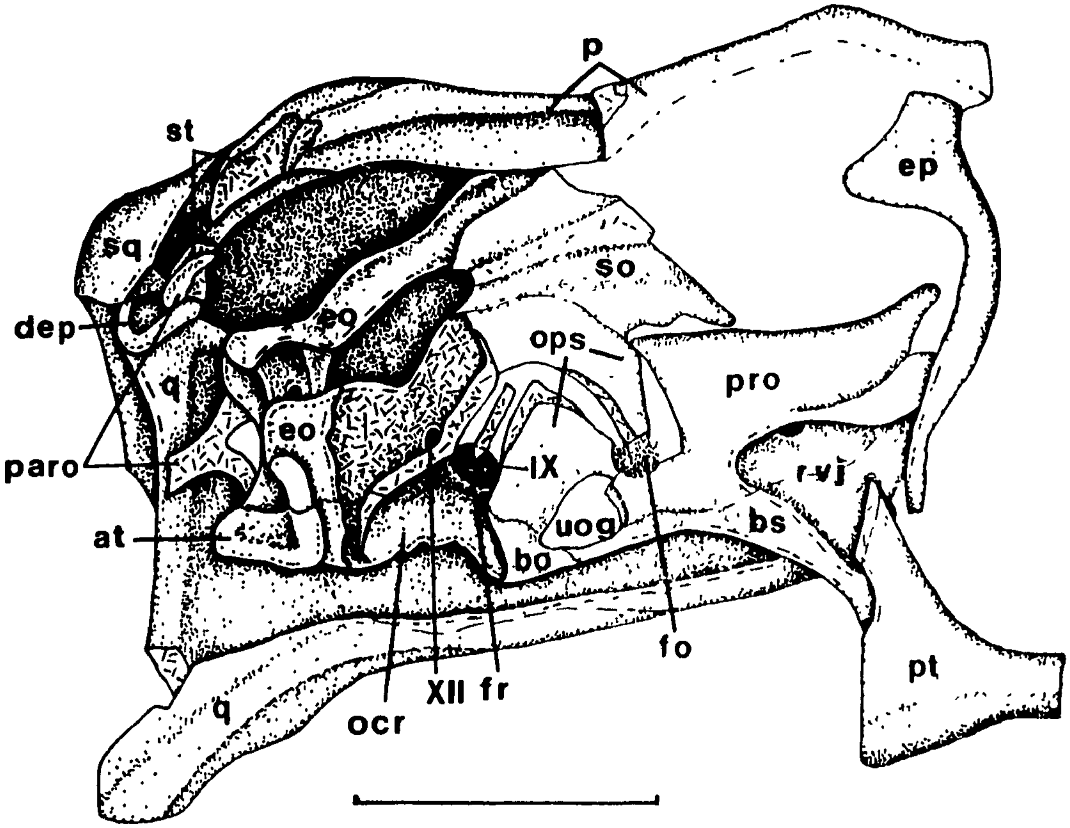
The unpaired basioccipital is almost complete except for the lateral surface. It forms the posteroventral part of the floor of the cranial cavity and the mid-part of the occipital condyle that articulated with the atlas. Anteroventrally, its suture with the parabasisphenoid is indistinct because of superficial erosion, but the basioccipital appears to be joined anteriorly by a tongue and groove suture to the parabasisphenoid. Anterolaterally, the basioccipital is expanded and turns dorsally to suture with the ventral process of the opisthotic and with the crista interfenestralis and the cresta tuberalis (Oelrich, 1956) of the exoccipital where it is drawn ventrally into a basal tubercle that is incomplete ventrally. The basal tubercle is deeply excavated dorsally into a fossa--the occipital recess (Oelrich, 1956). The occipital recess faces posterolaterally and forms part of the floor of the middle ear cavity. The crista tuberalis of the basioccipital is partially preserved on the left side. If it formed the posterior wall of the occipital recess as in most lizards, it would be broadly expanded laterally in life as reconstructed in figure 6. The basioccipital continuation of the crista interfenestralis contributes to the anterior wall of the occipital recess. As in Sphenodon, an unossified gap posteroventral to the fenestra ovalis remains between the basioccipital, the parabasisphenoid, the opisthotic and the prootic. A similar gap was described by Fraser in Clevosaurus (1988), but it does not involve the prootic in that genus.

The parabasisphenoid complex, formed by the fusion of the dermal parasphenoid with the ventral surface of the basisphenoid, is well-preserved. Posteriorly, it contributes to the anterior floor of the cranial cavity, anteriorly becomes a long, stout median cultriform process missing its anterior end. The ventral surface of the complex is constricted just posterior to the basipterygoid processes and broadens posteriorly. It extends laterally into a pair of processes that reach the basal tubera and overlap the basioccipital posteriorly. The paired basipterygoid processes are short but broad and laterally directed. The geometry of their articulating surface with the pterygoids suggests little movement at the basipterygoid joint. A pair of foramina for the internal carotid arteries are clearly evident between the basipterygoid processes. Posterolaterally, the sutures of the complex with the prootic and the basioccipital are very clear. In contrast with Clevosaurus, the bone does not meet the ventral process of the opisthotic along the border of the unossified gap. Anterolaterally, suture between the complex and the prootic is uncertain. It may reach the inferior process of the prootic based on common situation in Sphenodon and lizards.

The exoccipitals are incompletely fused to the opisthotics. The exoccipital is better-preserved on the right side except for the loss of the paroccipital process and the posterior surface that are preserved on the left side. It forms the lateral portion of the condyle and the posteroventral third of the otic capsule. Its suture of the bone with the basioccipital ventrally is clearly marked, but its suture with the supraoccipital dorsally is obscured in some region by surface erosion. Two openings in an incomplete basin between the left margin of the foramen magnum and the crista tuberalis are identified as the foramina for cranial nerve XII. Their inner openings are also seen within the cranial cavity. Another opening just dorsal to the basin is the foramen for the vagus nerve, cranial nerve X. Dorsal to the vagus foramen, a ridge extending from the lateral margin of the foramen magnum and ending on the paroccipital process divides the posterior surface of the exoccipital into dorsal (larger) and ventral (smaller) parts. A depression on the dorsal part probably served for the attachment of the supravertebral muscles.

Ventrolaterally, the right exoccipital shows a deep cavity that is a continuation of the occipital recess and forms with it a large atrium to a dorsally positioned opening. This large opening runs into the central cavity of the otic capsule and on its fully ossified medial wall a smaller opening pierces the bone into the cranial cavity. All features mentioned above demonstrate that the large opening is the fenestra rotundum and the smaller internal opening is the foramen for cranial nerve IX. The dorsal border of the fenestra rotundum is damaged and the central cavity of the right otic capsule is exposed because of the loss of the paroccipital process. The crista tuberalis and crista interfenestralis of the exoccipital are also incomplete. Anteriorly, the bone is medially compressed and disarticulated from the prootic so that the fenestra ovalis has lost its original configuration. Its appearance is further confused by the damage to the paroccipital process. Ventral to the fenestra rotundum and the fenestra ovalis the ventral process of the opisthotic borders the unossified gap anteroventrally.

Fig. 14. *Asiacephalosaurus wangi*, gen. et sp. nov. Posterior part of the skull in lateral view (slightly posterior), showing the braincase. Scale bar 5.0 mm.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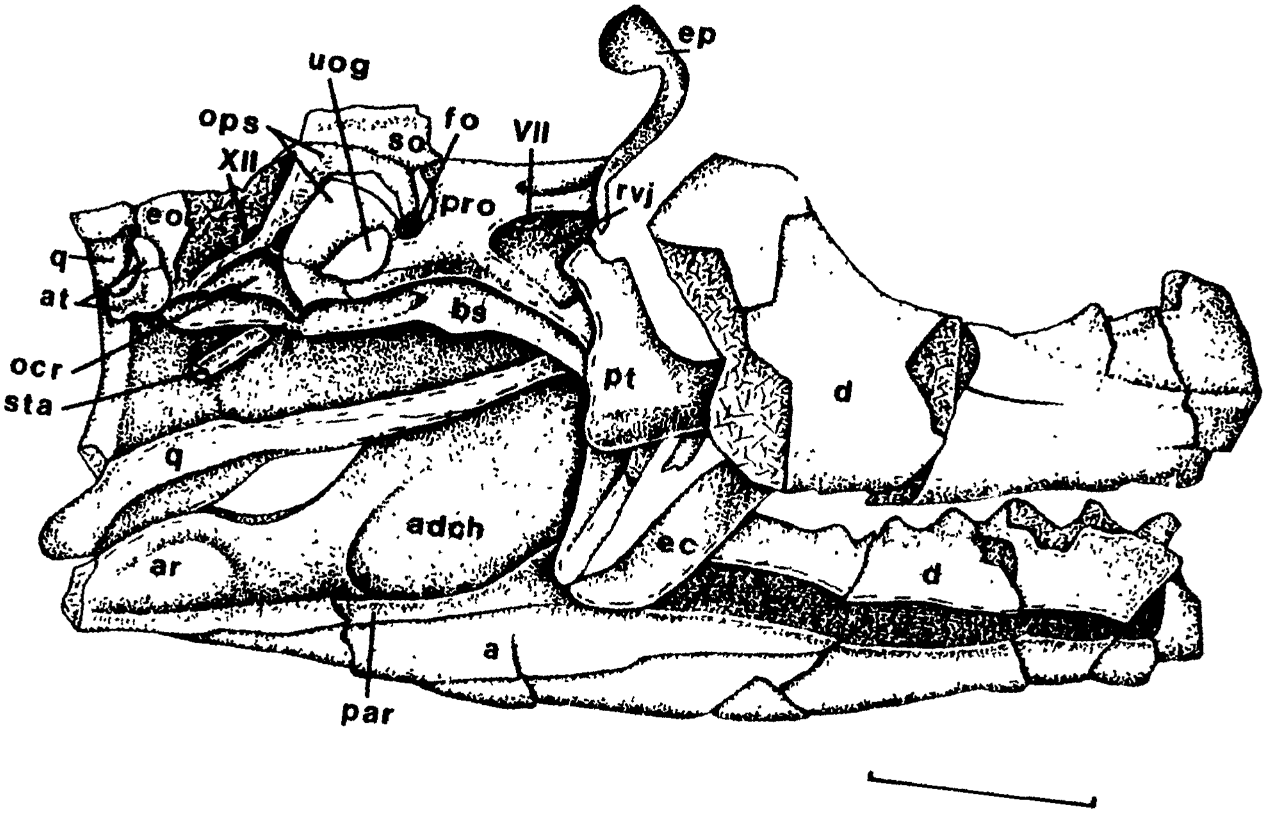
From the ventral process the crista interfenestralis arises between the fenestra rotundum and the fenestra ovalis as in the majority of extant lizards.

The paroccipital process on the left side was crushed distally and flattened medially. It is broken laterally, posteriorly and ventrally so that the central cavity of the otic capsule is exposed. Anteriorly, it must have been overlapped by the prootic and forms with the latter a paroccipital recess ventrally for the fenestra ovalis.

The supraoccipital is nearly complete except along both anterior and posterior margins. The element roofs the posterior part of the cranial cavity, forms the dorsal rim of the foramen magnum, and contributes to the anterodorsal third of the otic capsule. It is hexagonal in configuration and convex dorsally. Its suture with the exoccipital is indistinct in some regions. Anteriorly, it is disarticulated from the prootic. Dorsally, it probably joined the parietals through a cartilaginous junction. The lateral aspect of the bone slopes from a moderate median occipital crest that presumably served for the attachment of the ligament from the neck. On each side of the crest is a large depression that received the insertions of the muscles of the neck region.

The prootic is well-preserved on the right side although it has lost its posterodorsally directed process from which a crest forming the anterodorsal wall of the paroccipital recess is derived. The portion that forms the anterolateral surface of the cranial wall is slightly crushed dorsoventrally and

Fig. 15. Asiacephalosaurus wangi, gen. et sp. nov. Lateral view of the skull (slightly ventral), showing the medial aspect of the left mandible. Scale bar 5.0 mm.



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covered dorsally by matrix, thus reducing its exposure in lateral view. The bone makes up the anteroventral third of the otic capsule. Its articulation with the parietal may be similar to that of Sphenodon and extant lizards. The prootic probably makes contact with the dorsal end of the epipterygoid by a membranous junction. Posteroventrally, the bone forms the anterior rim of the unossified gap and further dorsally it shows a more or less semicircular notch that probably forms the anteroventral margin of the fenestra ovalis. Its crista alaris is not apparent anterodorsally. Its trigeminal notch is shallow, but the inferior process is very pronounced at the probable position of the suture with the parabasisphenoid. From the inferior process a pronounced ridge, the crista prootica, extends posteriorly and becomes indistinct more than half way to the fenestra ovalis. Below the crista prootica, the prootic is deeply excavated into a fossa, the recess vena jugularis, which expands ventrally onto the parabasisphenoid. The recess is distinct from that of extant lizards in that it does not expand posterodorsally to join the paroccipital recess. Near the posterodorsal margin of the recess vena jugularis there is a foramen through which cranial nerve VII goes forward into the orbital region.

f. Mandible (Figs. 7, 12, 13 and 15)

The left dentary is almost complete except for the symphysial region and the posterior tip. This tubular bone dominates the mandible. Generally it resembles that of other sphenodontidans. It bears a deep coronoid process and a distinctive elongated posterior process that tapers abruptly below the jaw articulation in this genus. At the midpoint between the last tooth and the jaw articulation, the small mandibular foramen for the recurrent nerve pierces the mandible at the dentary-surangular suture. Ventral to the dentition the dentary is thickened to resist the stress produced during occlusion. On its medial surface, an open Meckelian canal runs through the length of the bone. Anterior to the coronoid, the canal is bordered ventrally by the angular.

The left angular is incompletely preserved. As in Clevosaurus and Palaeopleurosaurus, the angular has more lateral exposure than is the case in Sphenodon. It curves posteriorly from its lateral contact with the dentary and surangular onto the ventral surface of the mandible, and then extends anterodorsally between the prearticular above and the dentary below onto the medial surface of the mandible. Anteriorly, the angular tapers along the ventral margin of the Meckelian canal. The bone seems to show a broad posterior termination on the basis of the broken surface.

The left coronoid is present but much of its surface is covered medially by the transverse flange of the pterygoid. The coronoid forms the medial part of the coronoid process. It has a small lateral exposure. Ventrally, the bone becomes very thin. Presumably, as in Sphenodon, the coronoid makes contacts with the anterior end of the prearticular and the dorsal margin of the angular ventrally to form the anterior border of the adductor chamber, although this region is not well exposed.

The articular, prearticular and surangular form a coossified complex, although the suture between the latter two is visible in certain area. The complex, missing only the retroarticular process, is well-preserved on the right side. It becomes transversely broad at the articular region.

The surangular forms most of the lateral surface posterior to the mandibular foramen and dorsal to the posterior process of the dentary. In medial aspect, the surangular goes from the dorsal region of the coronoid process back towards the articular to form the dorsal margin of the adductor chamber that is walled laterally by the dentary.

The position of the prearticular is indicated by a strap-like structure on the medial surface. Its posterior part expands dorsomedially to support the robust articular portion of the complex. It curves posteriorly from the contact with the angular onto the medial aspect, and then runs forwards to contribute to the ventral margin of the adductor chamber.

The articular is short but massive. It forms most of the articular facet (with a lateral contribution from the surangular), and contributes to the posterior margin of the adductor chamber. The dorsal condylar surface is divided by a ridge into a deep posteromedial fossa and a shallow anterolateral fossa, corresponding to the double quadrate condyle. Close articulation between the quadrate and articular precludes a more detailed description. The massive broken surface posteriorly suggests that the retroarticular process was probably well-developed as in other early sphenodontidans.

g. **Stapes** (Figs. 11 and 15)

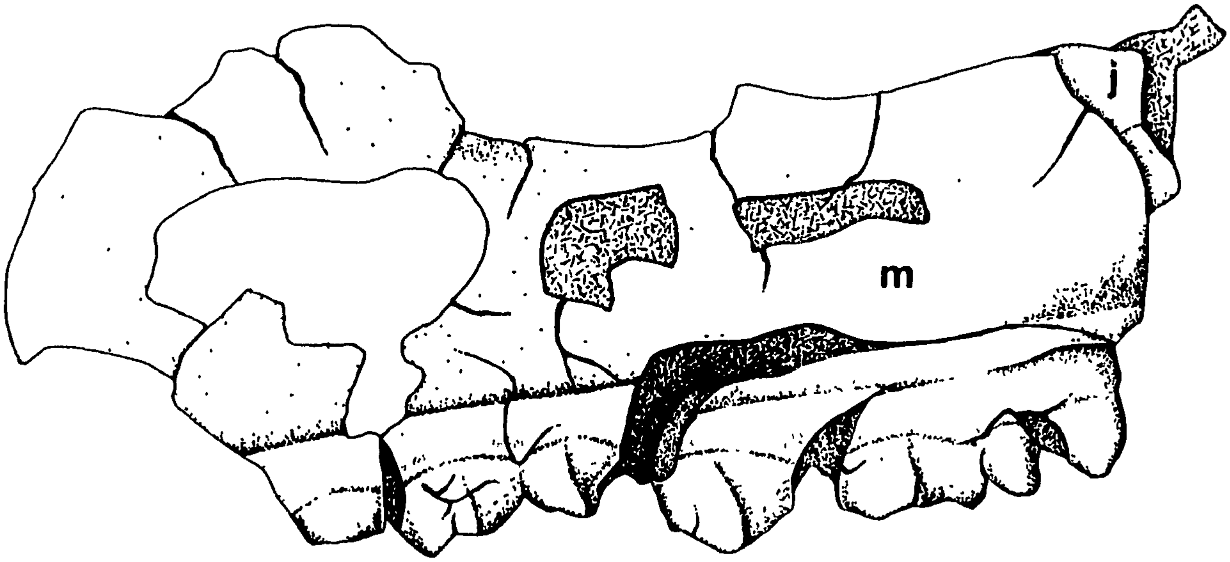
The left stapes is represented by two fragments. The proximal fragment is displaced with the distortion of the braincase and its footplate is covered by the paroccipital process. Towards the footplate the rodlike stump becomes thicker. The distal portion is positioned ventral to the paroccipital process. It is free from any bones and with a diameter of about 0.5 mm.

h. **Dentition** (Figs. 16, 7, 12 and 15)

No premaxillary teeth are preserved.

The left maxilla bears seven acrodont teeth somewhat damaged at the crowns. The first is small and subconical. It probably represents the remains of hatching teeth (Robinson, 1976). The four subsequent teeth progressively increase in size and are flanged posteriorly as in most sphenodontidans. They belong to the first series of the additional teeth (Robinson, 1976). The last two of the seven teeth are very small and conical. The first displays a very rudimentary flange posteriorly while the last is not fully ankylosed to

Fig. 16. Asiacephalosaurus wangi, gen. et sp. nov. Maxillary dentition in lateral (above) and occlusive (below) views. Scale bar 5.0 mm.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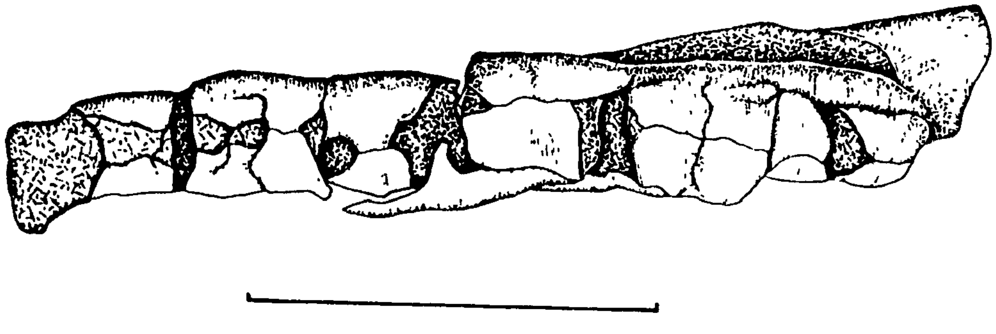

the bone medially. They probably represent the second series of the additional teeth. The maxillary dentition shows a considerable degree of tooth wear on the lingual surface.

The left dentary displays the most posterior six teeth in lingual view. The last two are smaller than the rest. The first is damaged anteriorly. All six teeth are flanged on both anterior and posterior sides. The anterior flanges are more pronounced than the posterior, as described by Fraser in Clevosaurus (1988). The labial aspect of the teeth is covered by the occlusion of the upper jaw. The dentition of the dentary has a similar pattern to that of maxilla: the first four teeth belong to the first series of the additional teeth, and the last small two represent the second.

As in Clevosaurus and Planocephalosaurus, the additional teeth of both maxilla and dentary do not alternate in size, which may demonstrate that the specimen is not a juvenile.

i. **Postcranial skeleton** (Figs. 11, 12, 14 and 15).

The only preserved elements of the postcranial skeleton are the intercentrum of the atlas and the ventral part of its right neural arch, which are still articulated with the basioccipital condyle.

The intercentrum is robust and very similar in appearance to that of Sphenodon. It is bowed slightly upwards on both sides so that its flat base is transversely convex ventrally. Its anterior and posterior margins are curved, but the latter is more greatly so than the former. The posterior surface is round, sloping and concave to receive the intercentrum of the axis. The anterior surface of the intercentrum, for articulation of the basioccipital condyle, is probably similar in appearance to that of the posterior, as in *Sphenodon*, except for the degree and direction of the sloping.

The remaining neural arch stands on the dorsolateral surface of the intercentrum. Its concave medial and bulging lateral aspects show that the neural arches on both sides may have formed a ring-shaped structure around the foramen magnum in life.

Rarojugalosaurus mcgilli

Systematic Paleontology

Rarojugalosaurus, gen. nov.

Type Species--Rarojugalosaurus mcgilli, gen. et sp. nov.

Etymology--Raro from Latin Rarus (rare, unusual), Jugalo from Latin Jugale (jugal), Rarojugalosaurus referring to the unusual jugal which has a dorsal process with an expanded extremity and the peculiar contact of its anterior process with the ventral process of the prefrontal anteriorly.

Diagnosis--A sphenodontidan differing from all others in having a jugal that possesses a long anterior process that meets the ventral process of the prefrontal at the anteroventral corner of the orbit, and a dorsal process that shows an expanded lateral exposure at its extremity; a postorbital that is greatly curved ventrally, showing a **T**-shaped outline. Many sphenodontidans are poorly known in palatal aspect, so the following feature may be either unique to the Rarojugalosaurus or shared with some others: the large row of palatine teeth is subparallel to the marginal teeth of the maxilla. The genus shares with Sphenodon a palatine that becomes broad and free posteriorly and a **L**-shaped suborbital fenestra. It shares with Clevosaurus and Asiacephalosaurus a posterodorsal process of the premaxilla that excludes the maxilla from the margin of the external naris. It shares with

Clevosaurus, Asiacephalosaurus and Dianosaurus a suborbital fenestra that is bordered by the palatine and ectopterygoid. It shares with Brachyrhinodon a short snout that is less than a quarter of the skull length.

Rarojugalosaurus mcgilli, sp. nov.

Holotype--V.8272: a skull with mandibles, but damaged in both snout and occipital region.

Paratype--V.8273: a skull lacking the post-orbital region, with the anterior parts of mandibles.

Locality--Near Dawa village, Lufeng county, Yunnan province, Southwest China.

Stratigraphic Position--About the middle of the upper part (Dark Red Beds) of the lower lufeng Formation (Layer 8 in table 4, see Sun et al., 1985).

Age--Probably Early Jurassic.

Etymology--A testimonial to McGill University, Montreal, Canada where I will have completed my Ph.D. training under the guidance of Professor Robert L. Carroll.

Diagnosis--As for genus.

Description

The holotype skull has been dorsoventrally compressed posterior to the orbit so that the braincase has been crushed. The basioccipital and antorbital regions are lost. The maxilla and jugal are not preserved on the right side. The skull table is heavily eroded along the midline. The mandibles are almost complet except for the symphysial region. In the paratype, the skull roof has been damaged, but the maxillae, the anterior tip of the snout, part of the right prefrontal and the elongated anterior process of the right jugal are preserved. The mandibles are complete anterior to the coronoid process. Of the palatal elements the palatine, the pterygoid and the ectopterygoid are present in the holotype and paratype.

The reconstructions of the skull are based on both holotype and paratype. As in Asiacephalosaurus, the complete lower temporal bar in the skull restorations is indicated by the expanded extremity of the descending process of the squamosal and its great ventral extension along the lateral side of the quadratojugal. Since Rarojugalosaurus is so closely related to Asiacephalosaurus, only the differences between them will be discussed in this description.

a. General features of the skull (Figs. 17--19)

The skull is about 2 cm long in the holotype, but up to 2.3 cm long in the paratype. It shows a relatively short and broad appearance in comparison with that of Asiacephalosaurus, which is indicated by its snout that reaches about 23% of the skull length. In this aspect, Rarojugalosaurus resembles Brachyrhinodon (Fraser and Benton, 1989). The supratemporal

Fig. 17. *Rarojugalosaurus mcgilli*, gen. et sp. nov. Composite reconstruction of the skull in dorsal view. Scale bar 5.0 mm.

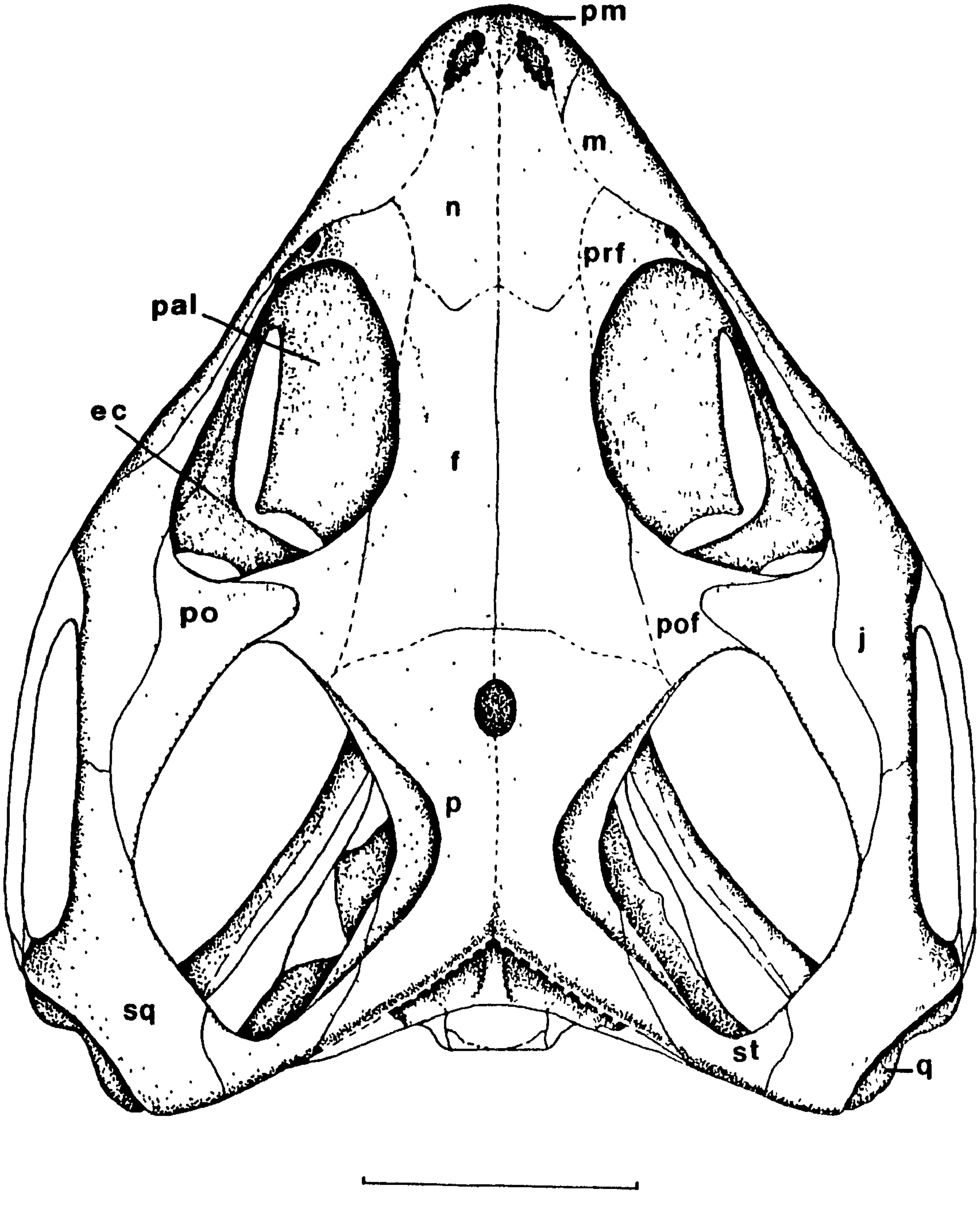
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Fig. 18. Rarojugalosaurus mcgilli, gen. et sp. nov. Composite reconstruction of the skull in lateral view. Scale bar 5.0 mm.

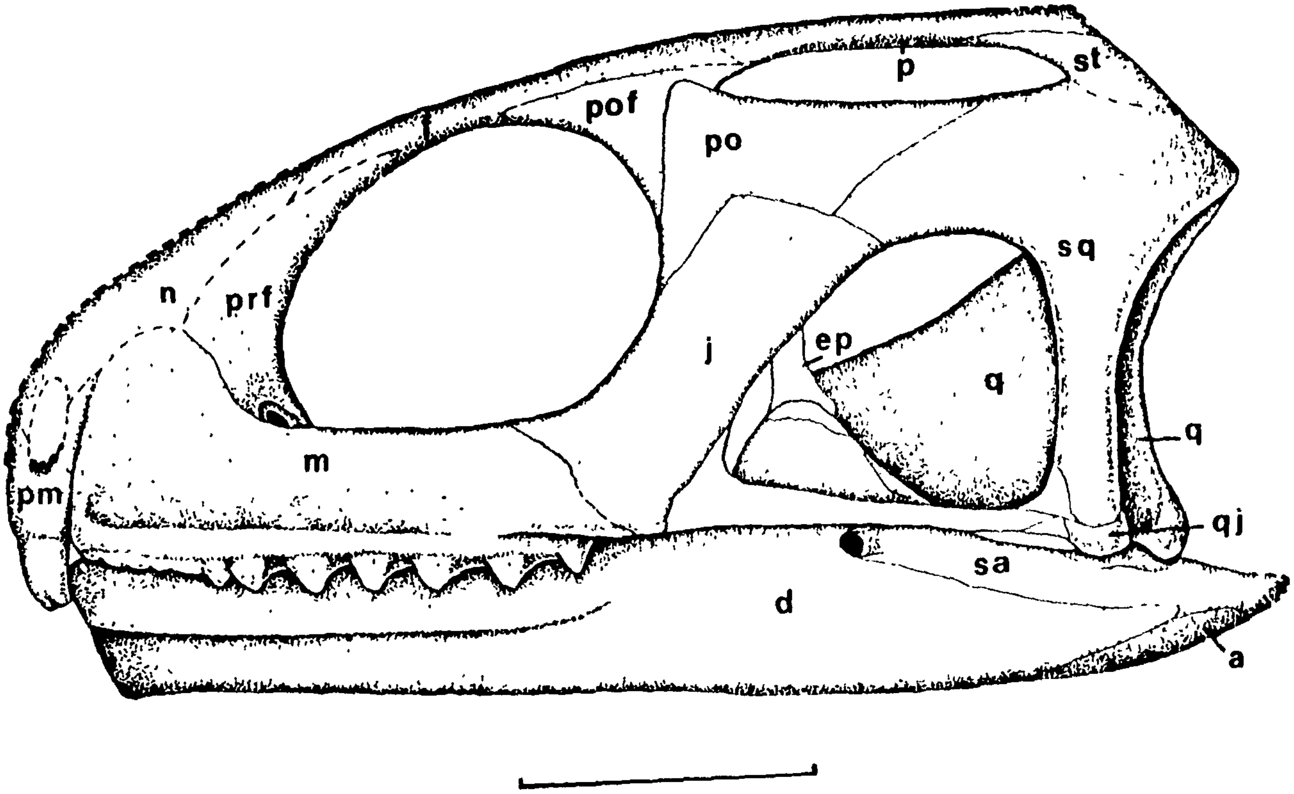
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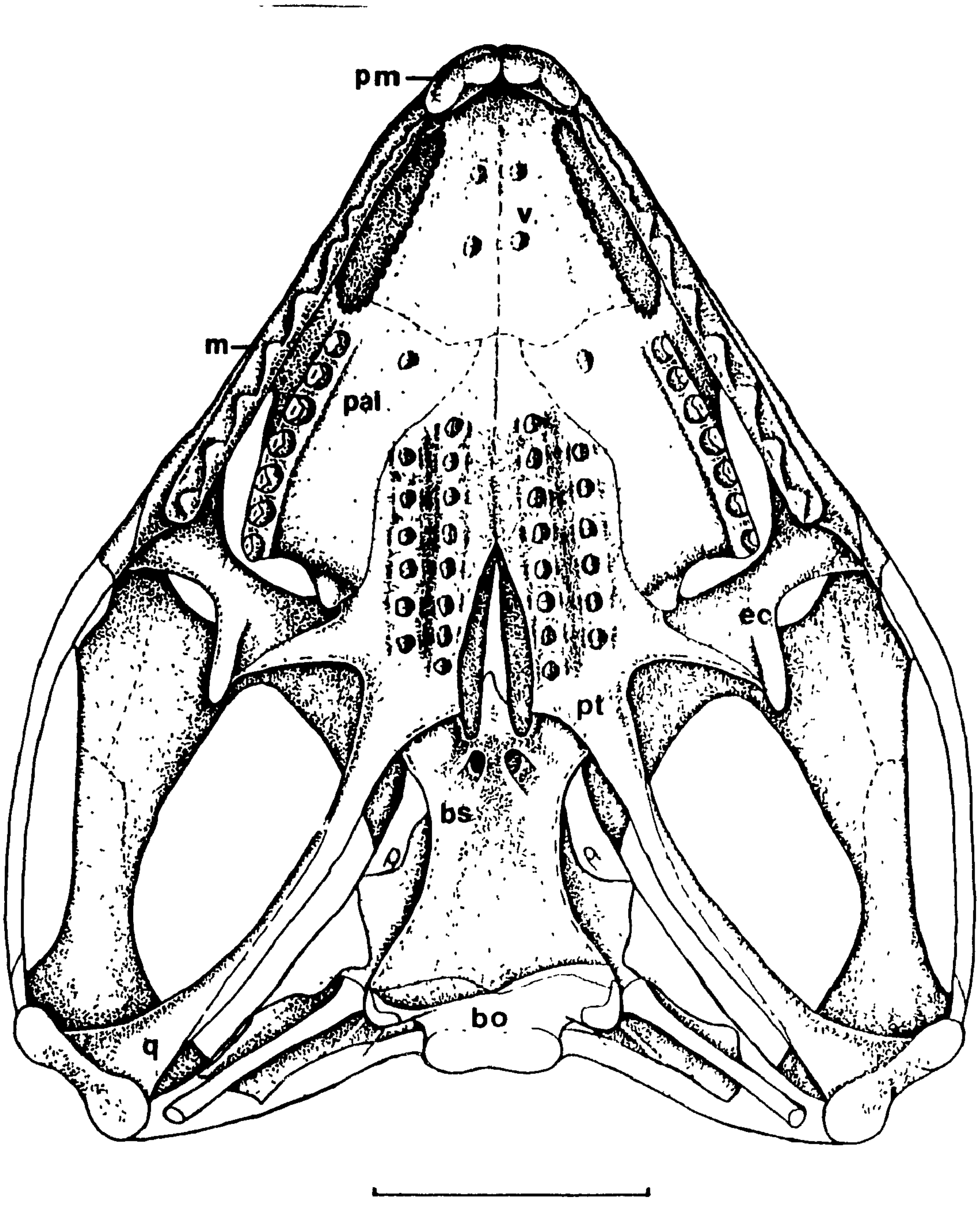
Fig. 19. Rarojugalosaurus mcgilli, gen. et sp. nov. Composite reconstruction of the skull in ventral view. Scale bar 5.0 mm.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fenestra is of rhombic shape and much larger than that of Asiacephalosaurus. It is most probably longer than the orbit, showing a considerable elongation of the temporal region. The suborbital fenestra is L-shaped as in Sphenodon.

b. Dermal bones of the skull roof (Figs.20--24)

Except for the sutures of the nasals to the premaxillae, the maxillae and the prefrontals, the relationships between the other bones of the skull roof are clearly marked, showing a pattern similar to that of Asiacephalosaurus. However, the following aspects are very different from the latter: the prefrontal shows a limited lateral exposure; the postorbital is T-shaped because of the great curvature of its ventral edge; the supratemporal displays an asymmetrical V-shaped configuration and does not extend posterolaterally along the medial margin of the squamosal to meet the paroccipital process; the parietals and the parietal table are greatly necked; as the size of the supratemporal fenestra indicates, the parietal table is much narrower than the interorbital width; and the jugal possesses an elongated anterior process that runs forwards along the ventral edge of the orbit to contact the ventral process of the prefrontal and a relatively short dorsal process with an expanded extremity that fits in the concave ventral margin of the postorbital. In addition, the supratemporal bar is greatly narrowed by the expansion of the supratemporal fenestra. Although the parietals were damaged

Fig. 20. Rarojugalosaurus mcgilli, gen. et sp. nov. Dorsal view of the type skull. Scale bar 5.0 mm.

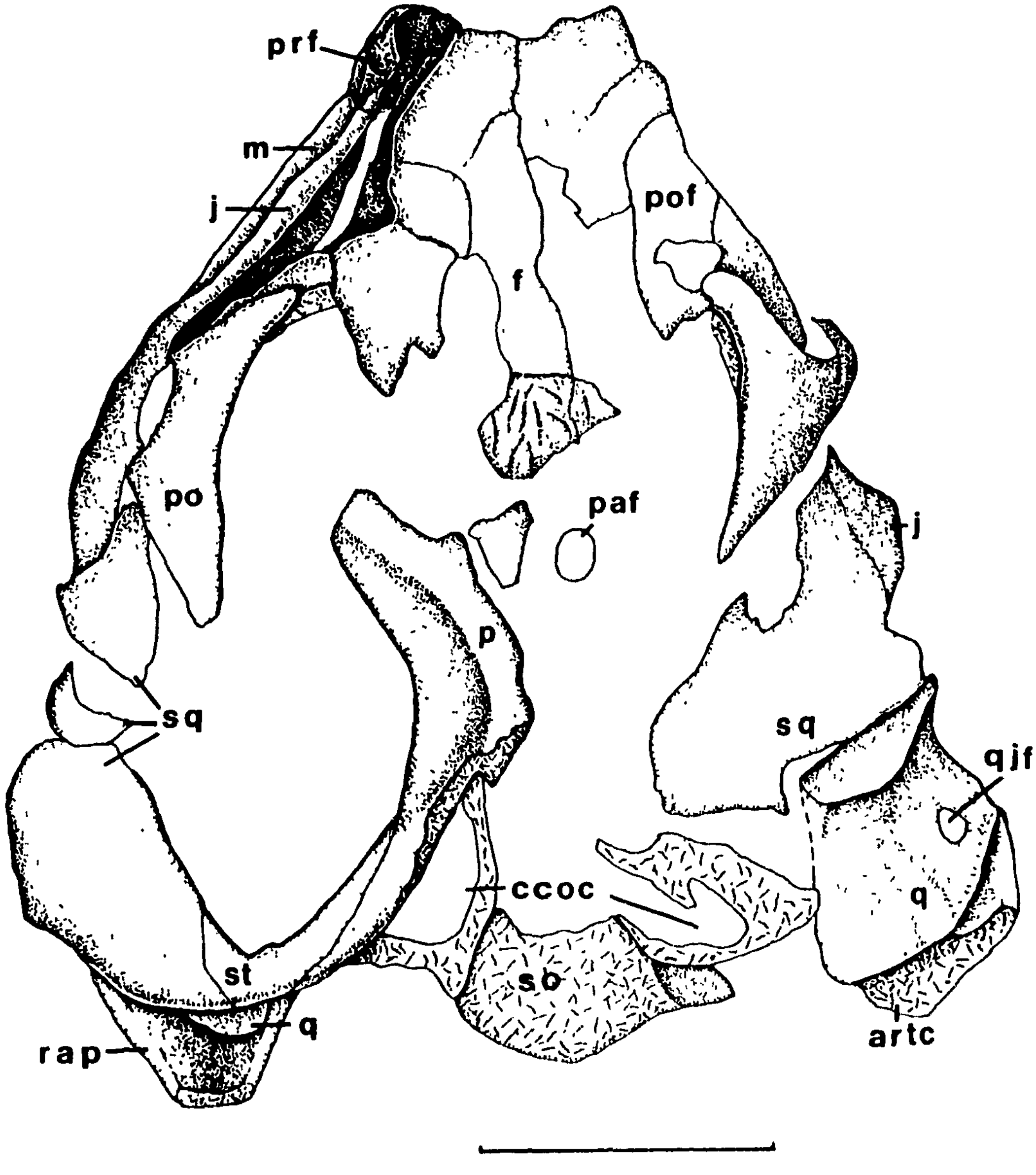
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Fig. 21. <u>Rarojugalosaurus</u> <u>mcgilli</u>, gen. et sp. nov. Lateral view of the paratype skull. Scale bar 5.0 mm.

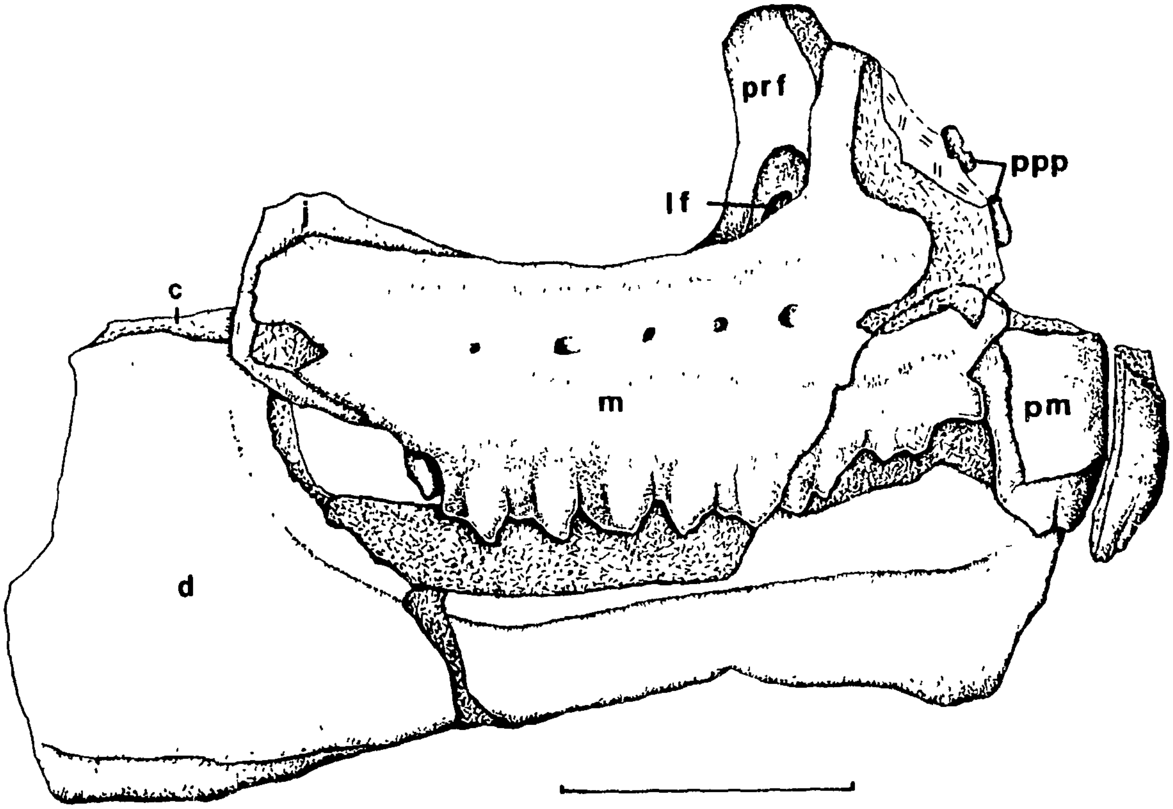
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Fig. 22. Rarojugalosaurus mcgilli, gen. et sp. nov. Lateral view of the type skull. Scale bar 5.0 mm.

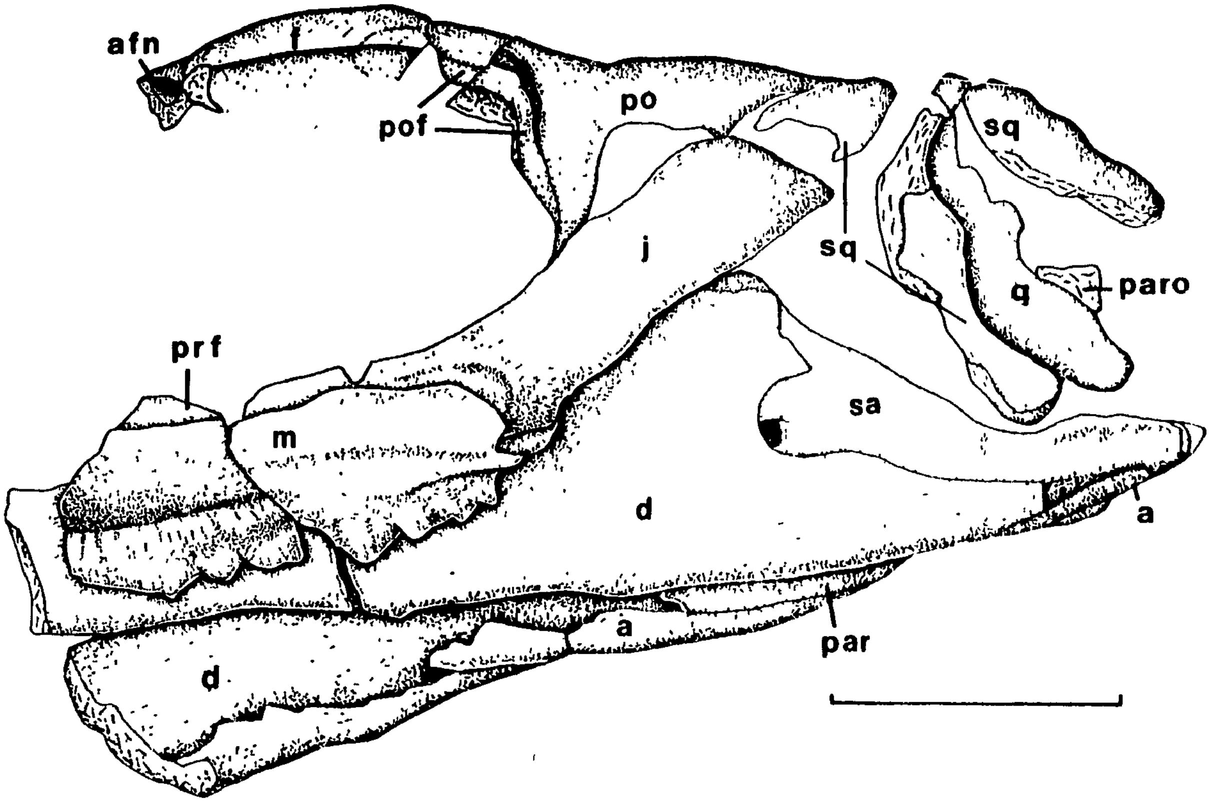
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Fig. 23. *Rarojugalosaurus mcgilli*, gen. et sp. nov. Dorsal view of the paratype skull. Scale bar 5.0 mm.

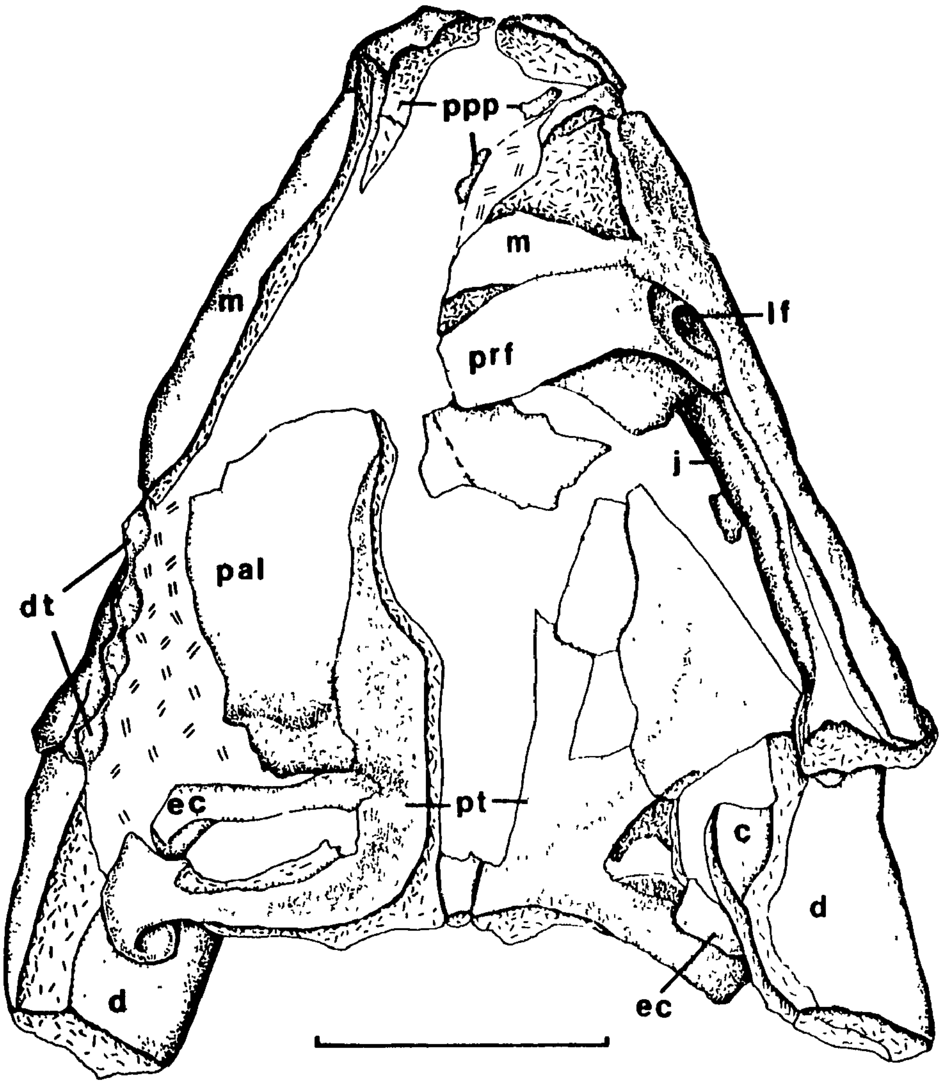
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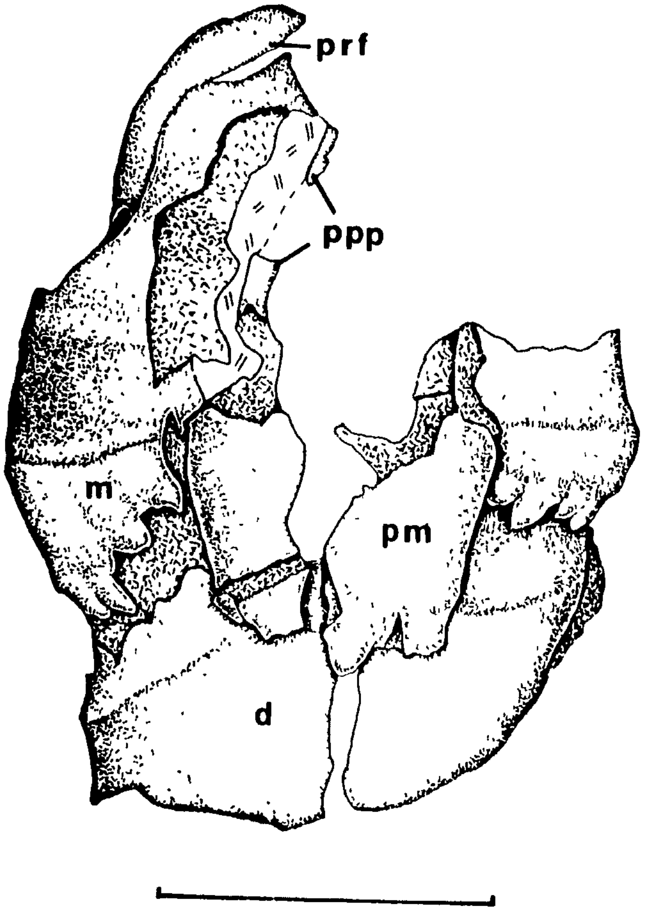
Fig. 24. Rarojugalosaurus mcgilli, gen. et sp. nov. Anterior view of the paratype skull. Scale bar 5.0 mm.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along the midline, the position and size of the parietal foramen can be determined by fillings that show different colour from that of the surrounding matrix. The foramen does not reach the line between the anterior margins of the supratemporal fenestrae as in Clevosaurus.

c. Palatoquadrate (Figs. 20, 22 and 25)

The quadrate is very distinct from that of Asiacephalosaurus in that the cephalic head is convex and fits into a matching depression on the ventral surface of the squamosal and is separated by the latter from the paroccipital process as in most other sphenodontidans.

The epipterygoid is not exposed.

d. Dermal bones of the palate (Figs. 23 and 26--28)

The vomers are not preserved in either the holotype or the paratype. The palatine is very similar to that of Sphenodon in that the bone is broadened and free posterolaterally, resulting in a L-shaped suborbital fenestra and the subparalleling of the lateral row of the large palatine teeth to the maxillary dentition. A pronounced tooth-like tubercle is formed at the suture with the pterygoid and ectopterygoid in Rarojugalosaurus, Sphenodon and Clevosaurus (Fig. 15 of Plate 3, Fraser, 1988). In contrast to that of Asiacephalosaurus, the central region between three rami of the

Fig. 25. *Rarojugalosaurus mcgilli*, gen. et sp. nov. Occipital view of the type skull. Scale bar 5.0 mm.

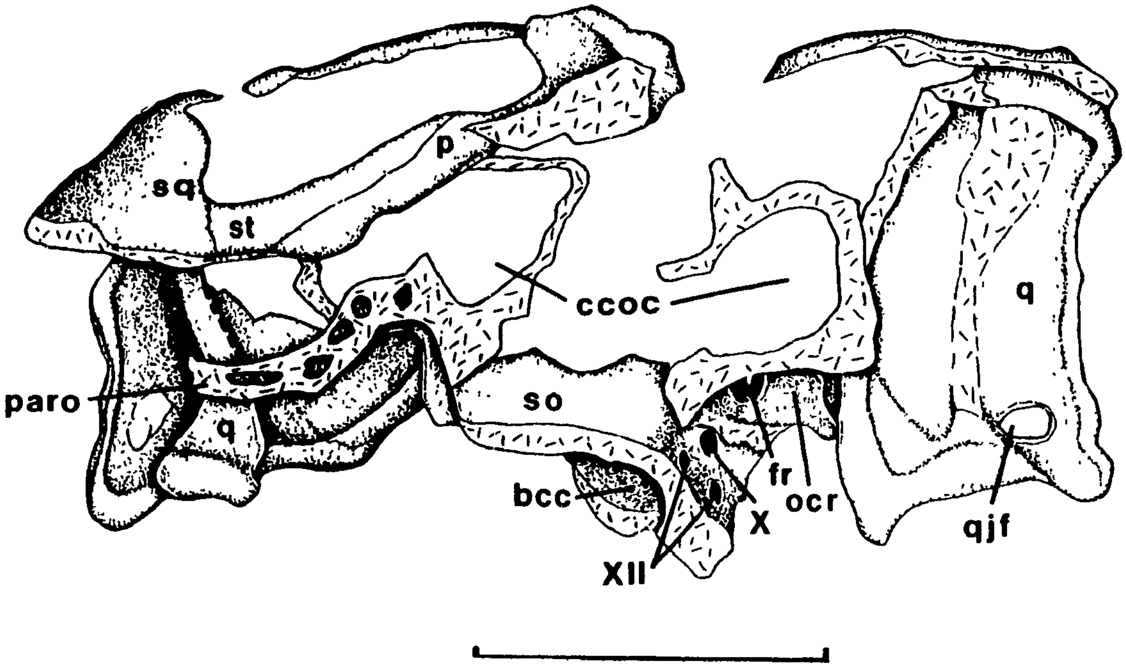

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Fig. 26. *Rarojugalosaurus* *mcgilli*, gen. et sp. nov. Antorbital region of the type skull in dorsal view, showing the relationships between the jugal and the prefrontal and between the palatine and the ectopterygoid. Scale bar 5.0 mm.

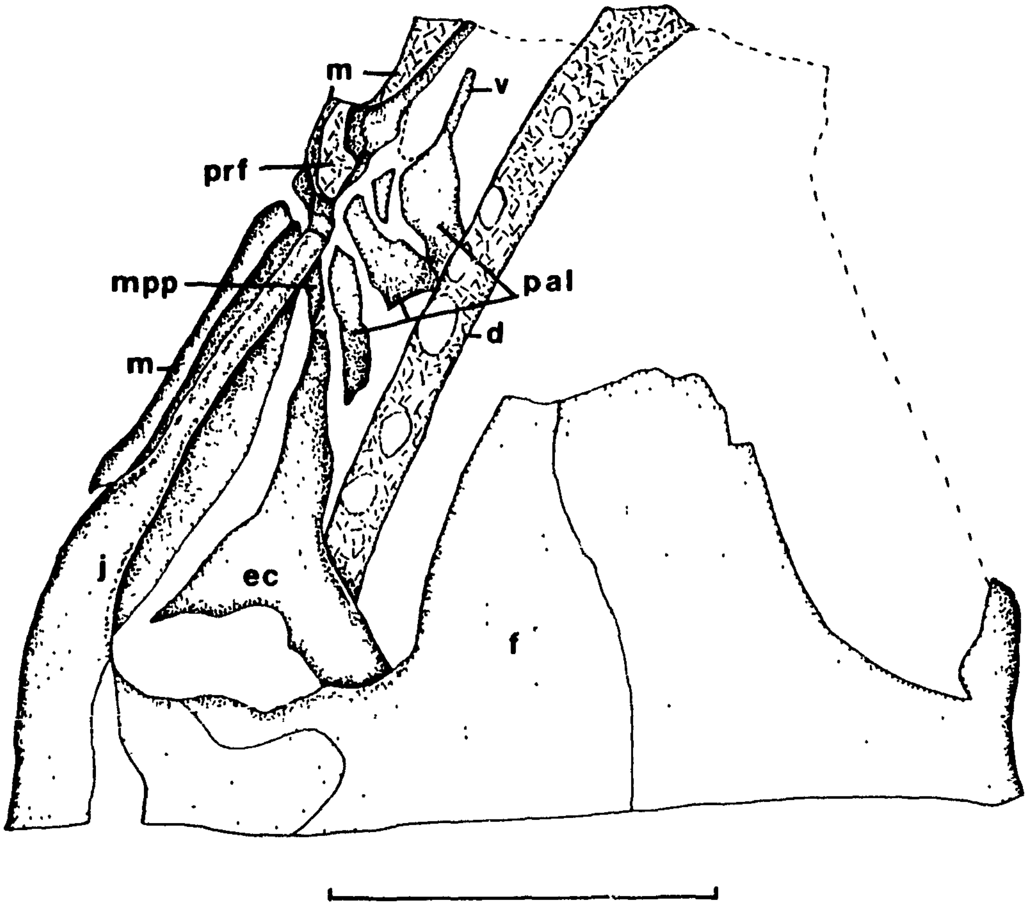
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Fig. 27. *Rarojugalosaurus mcgilli*, gen. et sp. nov. Ventral view of the type skull. Scale bar 5.0 mm.

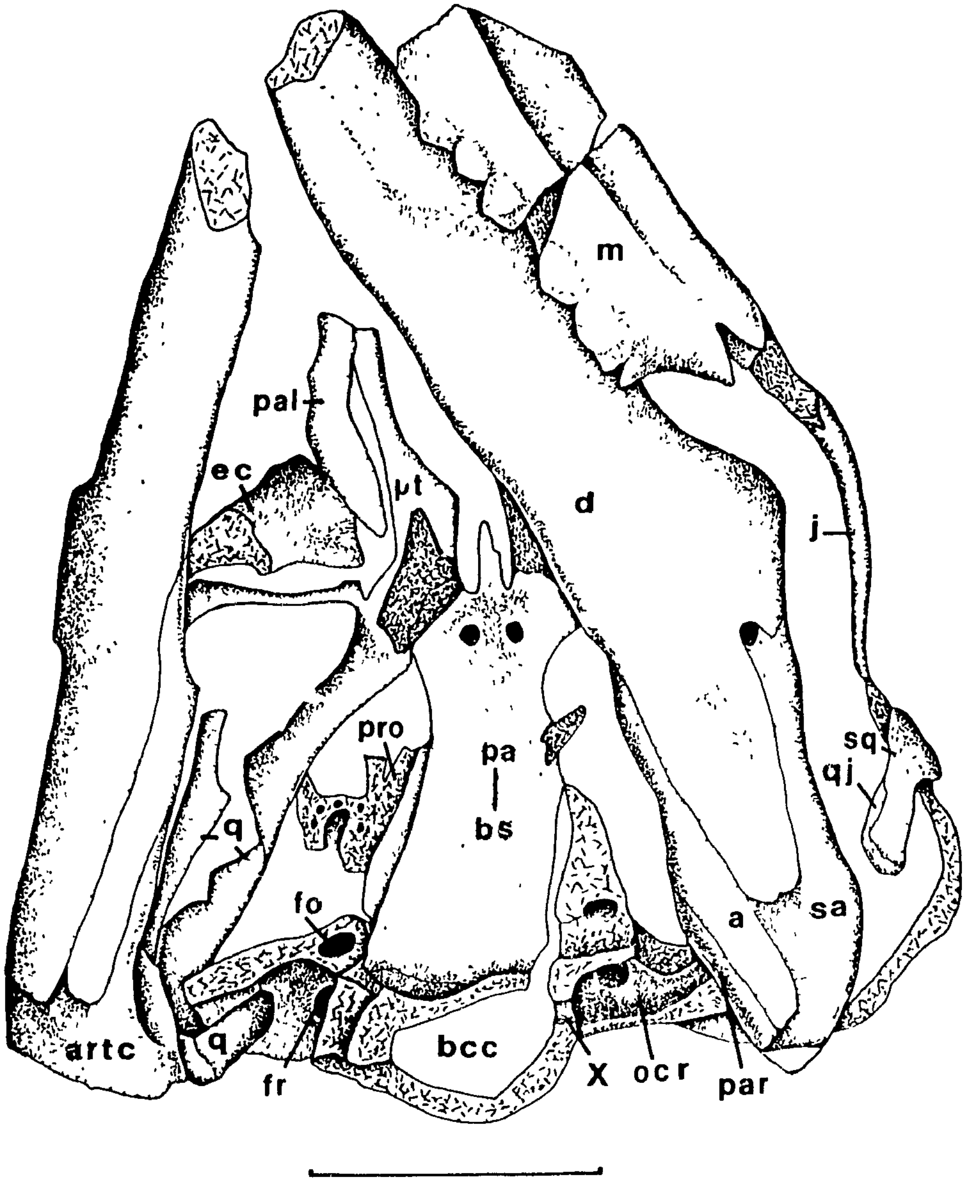
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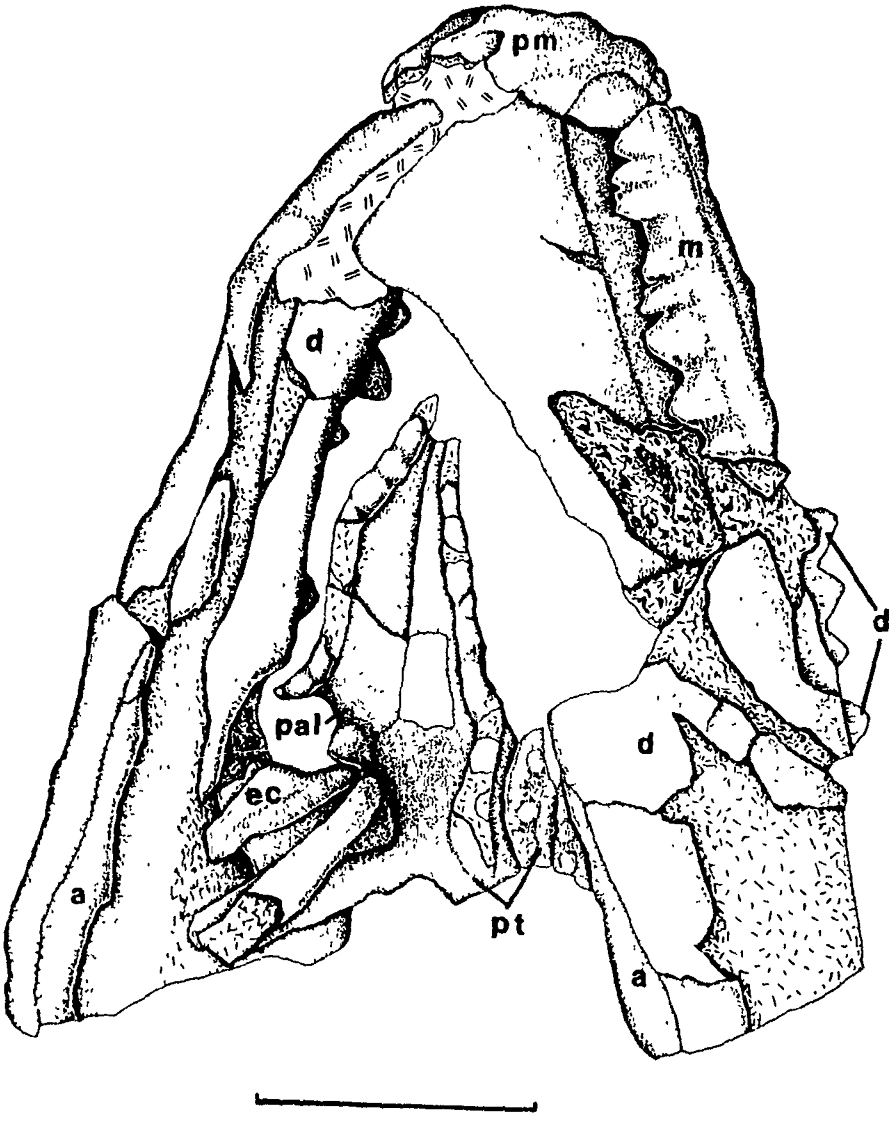
Fig. 28. Rarojugalosaurus mcgilli, gen. et sp. nov. Ventral view of the paratype skull. Scale bar 5.0 mm.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pterygoid is not elongated as in most other sphenodontidans.

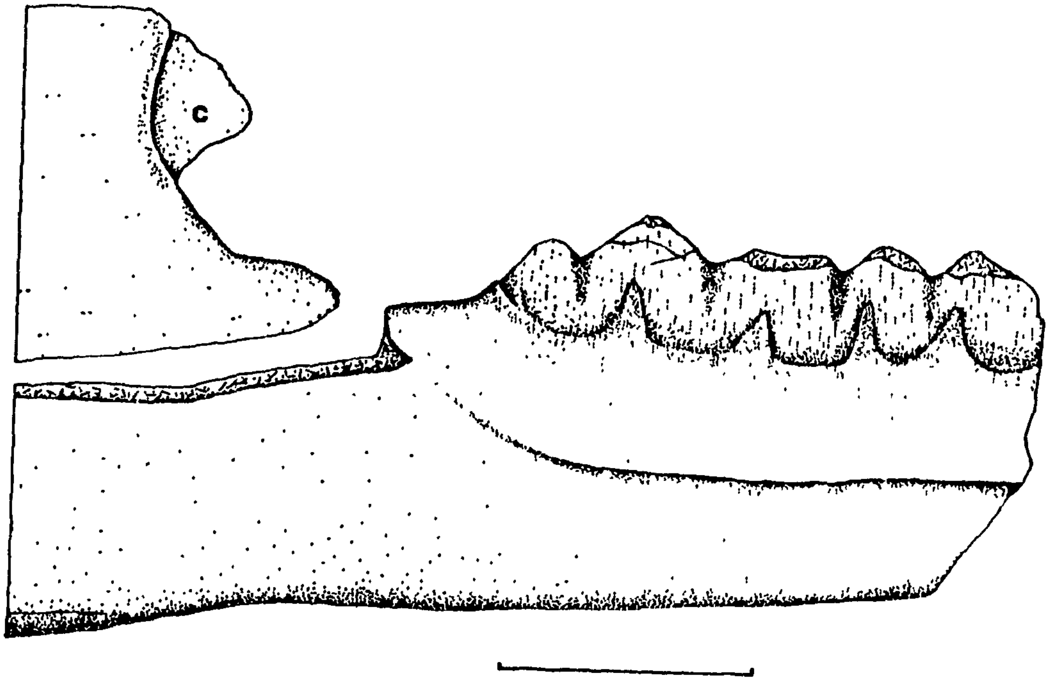
e. Braincase (Figs. 20, 25 and 27)

The braincase is very fragmentary. Of the bones of the braincase, only the parabasisphenoid is well enough preserved to warrant description. The complex is relatively long in comparison to that of Asiacephalosaurus and does not have any depressions or fossae on its ventral surface. The left paroccipital process shows on the broken surface a series of airspaces that are not present in Asiacephalosaurus.

f. Mandible (Figs. 21--24 and 25--29)

The mandible shows no significant differences from that of most other sphenodontidans. However, unlike in Asiacephalosaurus, the posterior process of the dentary tapers gradually beyond the mandibular foramen. The symphysis of the dentary (not preserved in Asiacephalosaurus) is very broad as in Clevosaurus. The retroarticular process (damaged in Asiacephalosaurus) is well-developed. It forms on its dorsal surface a central depression rimmed by a raised margin. The lateral margin of the rim contributes to the tympanic crest for the attachment of the tympanum, while the medial margin serves as the insertions of the M. pterygoideus typicus. The posterior extremity of the process for the attachment of the M. depressor mandibulae is missing.

Fig. 29. Rarojugalosaurus mcgilli, gen. et sp. nov. Posterior dentary dentition of the type skull in lateral view. Scale bar 5.0 mm.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g. **Dentition** (Figs. 21--24 and 27--29)

The premaxillary dentition is not known in Asiacephalosaurus. In Rarojugalosaurus, the premaxilla of the paratype bears two teeth on each side but their crowns on the right side have been damaged. The teeth are conical and of similar size. As in Sphenodon and Clevosaurus, the teeth overhang the tip of the mandible to form a beak-like structure on the rostrum.

The maxillary dentition, seen in the paratype, is slightly different from that of Asiacephalosaurus in that there is an additional series of five equal-sized teeth. The right dentary of the holotype bears the posteriormost five teeth. As in Clevosaurus and Palaeopleurosaurus, the lateral aspects of the teeth display many vertical score lines that continue across the surface of the dentary. This demonstrates that the early sphenodontidans had not developed propalinal jaw movements (Fraser, 1988).

Dianosaurus petilus Young, 1982

History of Study

Dianosaurus petilus was described by Young in a posthumous paper in 1982 based on an incomplete skull with mandibles (V.4007). Young believed that D. petilus did not possess an inferior temporal fenestra and consequently he placed it in the subclass Euryapsida of Romer's classification. Having considered the impossibility of an aquatic life, Young referred it to the order Protorosauria. Since D. petilus has no dental features comparable to those of the Trilophosauridae, which is the only Late Triassic family of the Protorosauria, and differs in many other aspects from the known protorosaurs, Young doubted his systematic assessment of the species in the same paper and pointed out that D. petilus might represent a new taxon of reptiles so far unknown in Lufeng area. Although he created a new genus and new species for the skull, Young failed to establish any generic or specific distinctions.

The current study of the skull reveals that Young erred in his description of a number of significant systematic characters that clearly indicate a sphenodontidan status of D. petilus as a new genus and species of the Sphenodontida.

Systematic Paleontology

Dianosaurus Young, 1982

Type Species--*Dianosaurus petilus* Young, 1982.

Diagnosis--A sphenodontidan differing from all others in having oval supratemporal fenestrae that are diagonally oriented, a jugal with a very short anterior process, and a pair of very slender basipterygoid processes. It shares with *Clevosaurus*, *Asiacephalosaurus* and *Rarojugalosaurus* a suborbital fenestra that is solely enclosed by the palatine and the ectopterygoid. It shares with *Clevosaurus* a parietal width that is narrower than the interorbital region. It shares with *Sphenodon* the dorsal margin of the maxilla that extends dorsally at the posteroventral corner of the orbit. It shares with *Asiacephalosaurus* a semicircular depression on the ventral surface of the parabasisphenoid complex. It shares with *Gephyrosaurus* a prearticular that extends anteriorly beyond the ventral margin of the coronoid to contribute to ventral border of the Meckelian canal.

Dianosaurus petilus Young, 1982

Holotype--V.4007: a skull with mandibles, damaged anterior to the orbits.

Locality--Close to Dachong village, Lufeng county, Yunnan province, Southwest China.

Stratigraphic Position--Near the top of the lower part (Dull purplish Beds) of the Lower Lufeng Formation (Layer 6, see Sun et al., 1985).

Age--Probably the Latest Triassic.

Diagnosis--As for the genus.

Redescription

The left side of the skull is not well-preserved. The right supratemporal fenestra is distorted; the lower temporal bars are broken. The braincase was damaged, especially in the posterior region.

The current study shows that *Dianosaurus* resembles both *Asiacephalosaurus* and *Rarojugalosaurus* collected from the same area. As a result, the description of *Dianosaurus* is centred on the differences between it and the other two Lufeng genera.

a. General features of the skull (Figs. 30--32)

The skull is approximately 3.5 cm long, with an appearance similar to that of *Asiacephalosaurus* and *Clevosaurus*. The supratemporal fenestra is relatively much larger than that of *Asiacephalosaurus*. Its major axis is not parallel to but oblique to the midline although comparable in both size and configuration to that of *Rarojugalosaurus* and *Clevosaurus*. The diagonal orientation of the supratemporal fenestra was reconstructed by Fraser and Benton (1989) for

Fig. 30. *Dianosaurus petilus*. Reconstruction of the skull in dorsal view. Scale bar 5.0 mm.

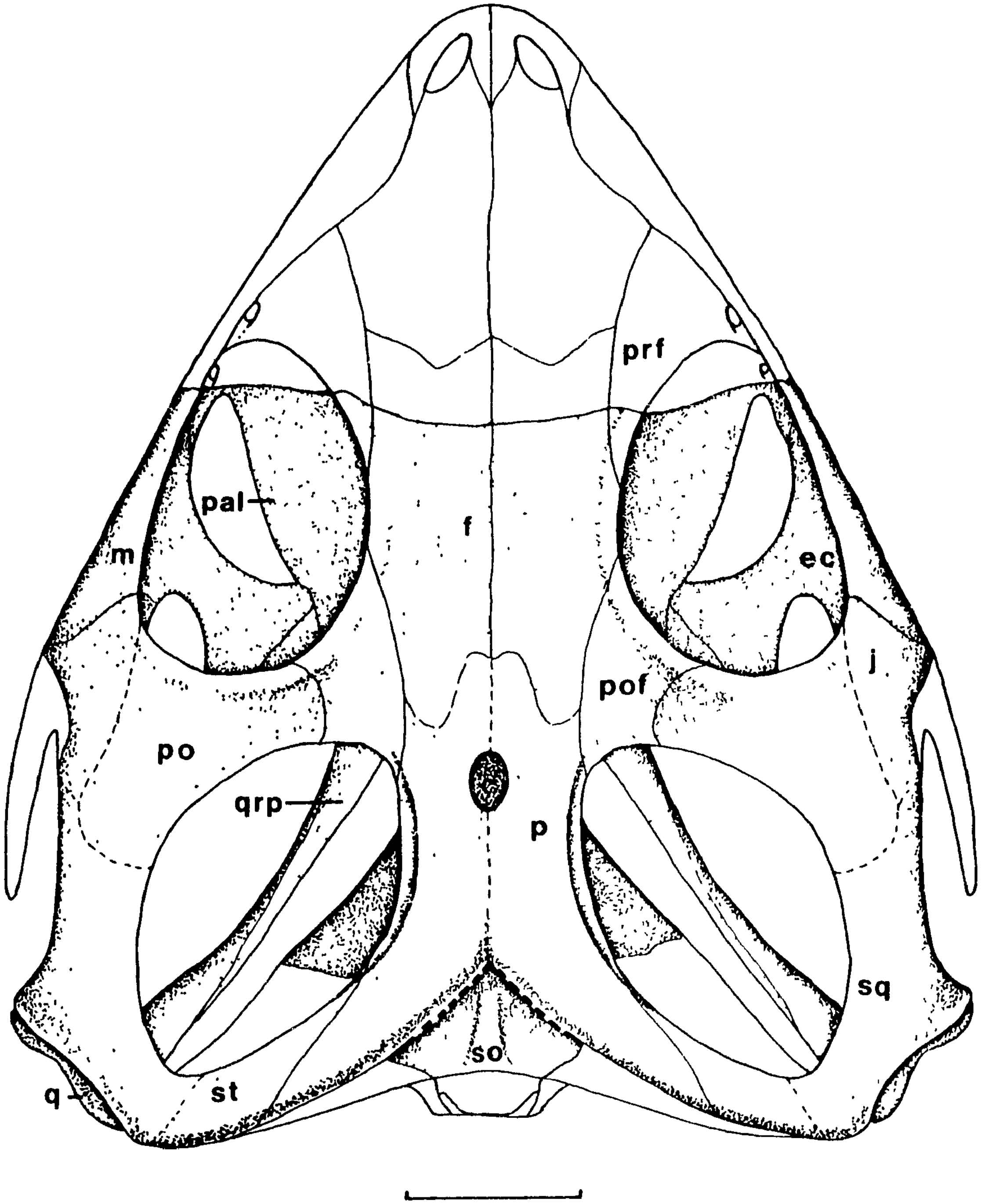
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Fig. 31. *Dianosaurus petilus*. Reconstruction of the skull in lateral view. Scale bar 5.0 mm.

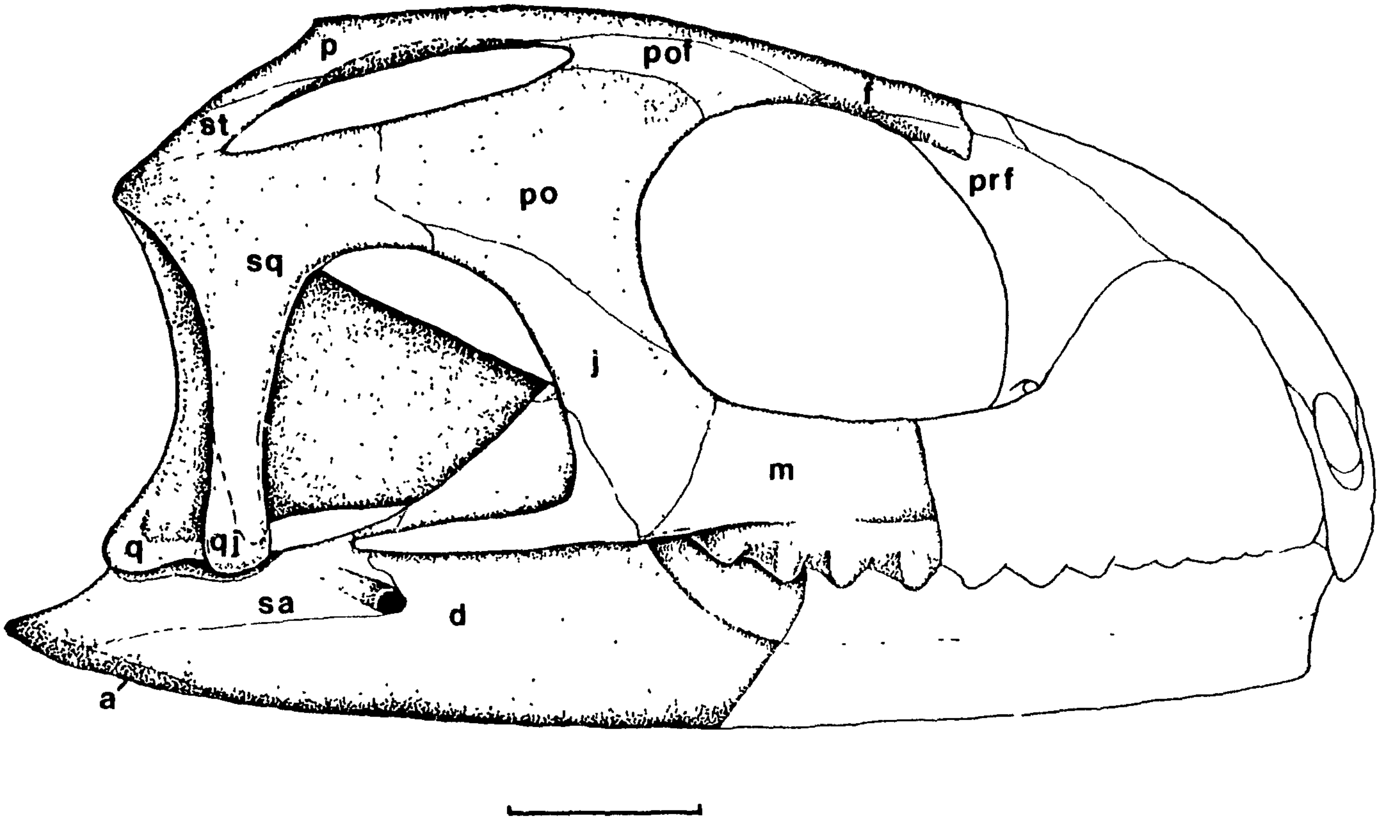
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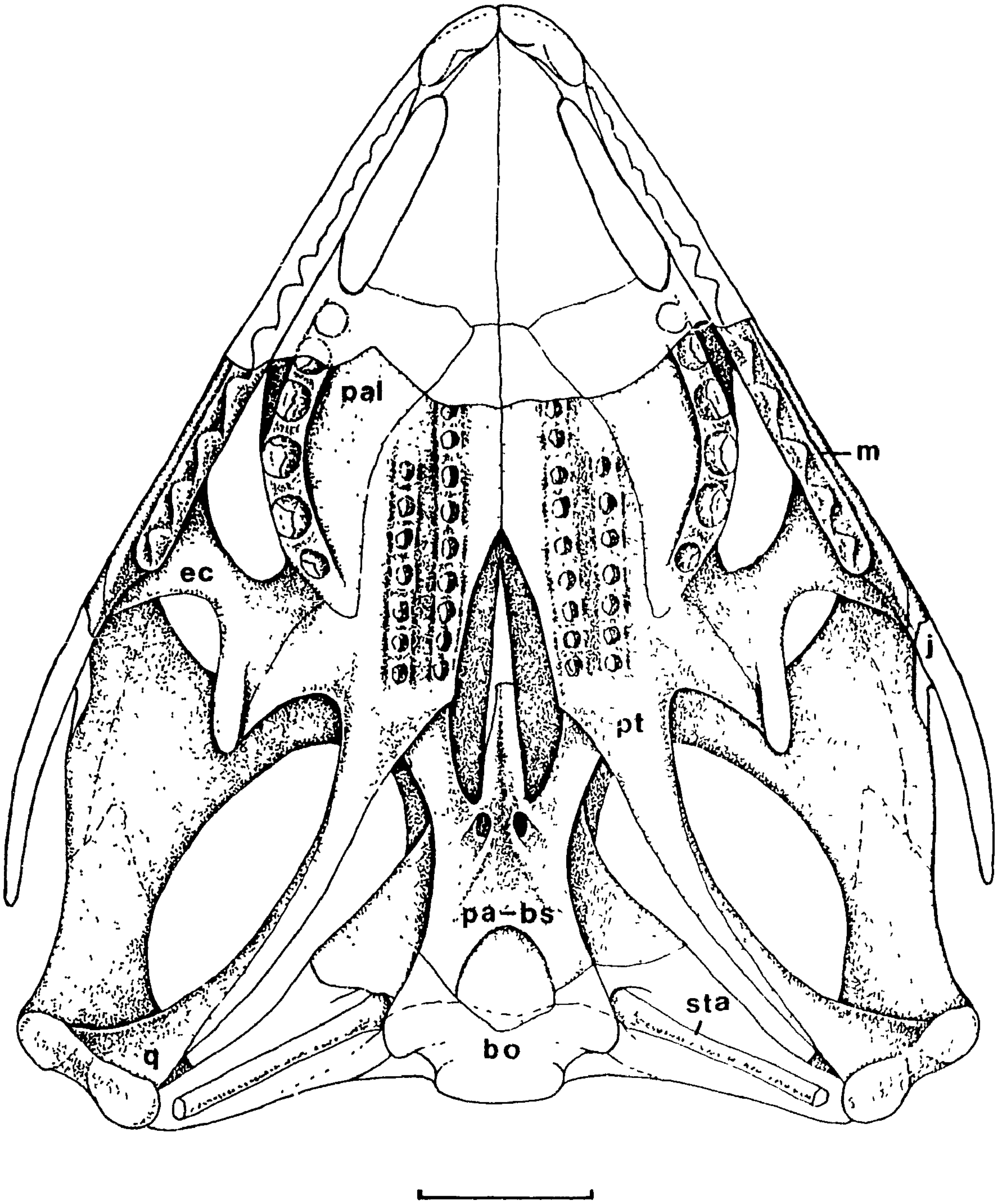
Fig. 32. Dianosaurus petilus. Reconstruction of the skull in ventral view. Scale bar 5.0 mm.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Brachyrhinodon (Huene, 1910). However, their figure 2 of the original specimen (BMNH R3559) shows that the preserved anterior half of the supratemporal fenestra has an orientation parallel to the midline as in most other sphenodontidans. It is difficult to determine whether the lower temporal bar is complete in Dianosaurus. The antorbital region of the skull is reconstructed on the basis of that of the other two genera from the Lufeng Basin.

b. Dermal bones of the skull roof (Figs. 33--35)

In contrast to that of Asiacephalosaurus and Rarojugalosaurus, the parietal is not broad anteriorly and the parietal width between the supratemporal passages is narrower than the interorbital region as in Clevosaurus. Since the bone does not form a moderate-sized medial shelf of the supratemporal fenestra laterally, the parietal table is broader than that of Rarojugalosaurus. The suture of the parietals to the frontals is more or less W-shaped. The supratemporal is probably present as indicated by the small size of the medial process of the squamosal of Asiacephalosaurus, Rarojugalosaurus and Clevosaurus. Nevertheless, its relationship to the squamosal or the paroccipital process or the quadrate cephalic head remains uncertain in Dianosaurus. The jugal is distinct from that of Asiacephalosaurus and Rarojugalosaurus in that its restricted anterior process only forms a small portion of the

Fig. 33. Dianosaurus petilus. Dorsal view of the skull. Scale bar 5.0 mm.

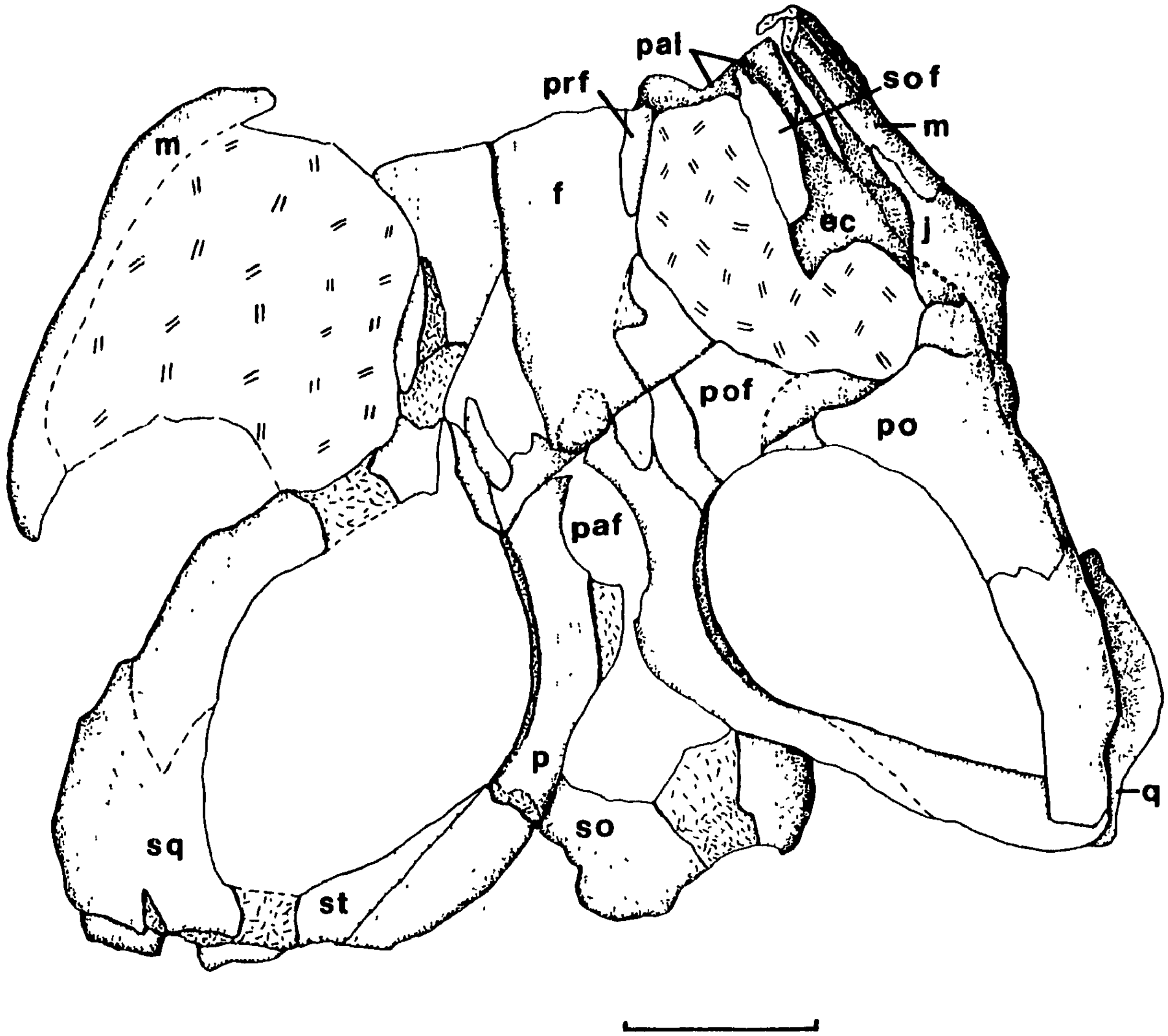
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Fig. 34. Dianosaurus petilus. Lateral view of the skull. Scale bar 5.0 mm.

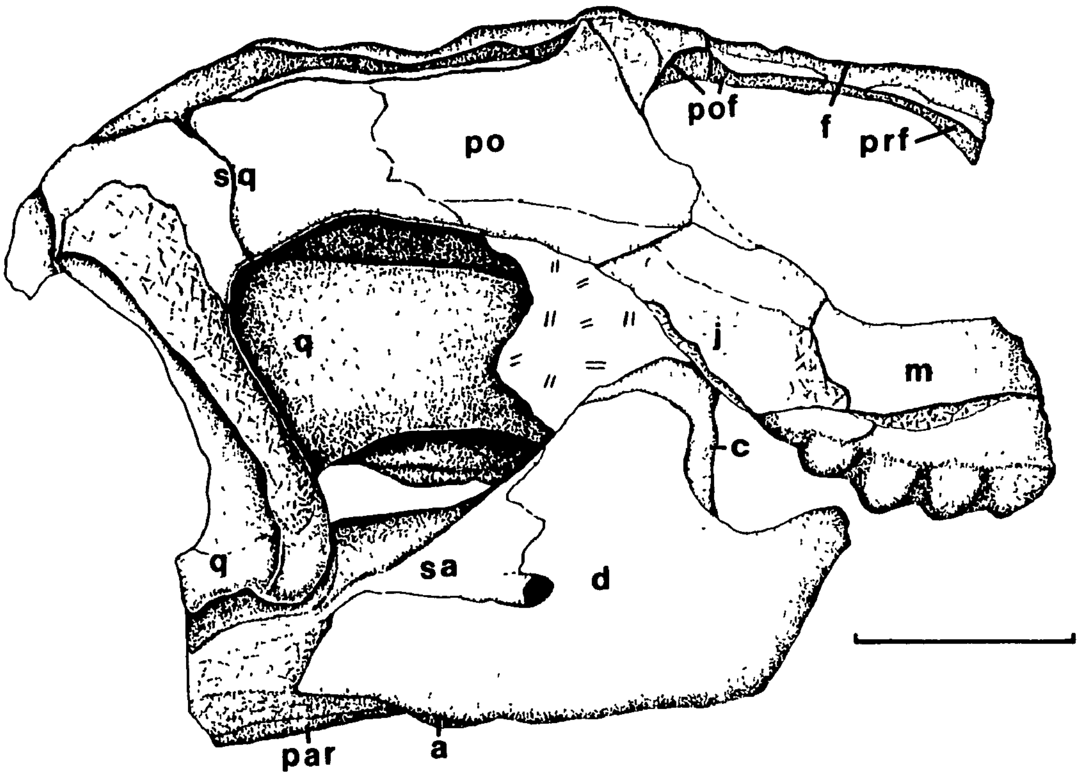
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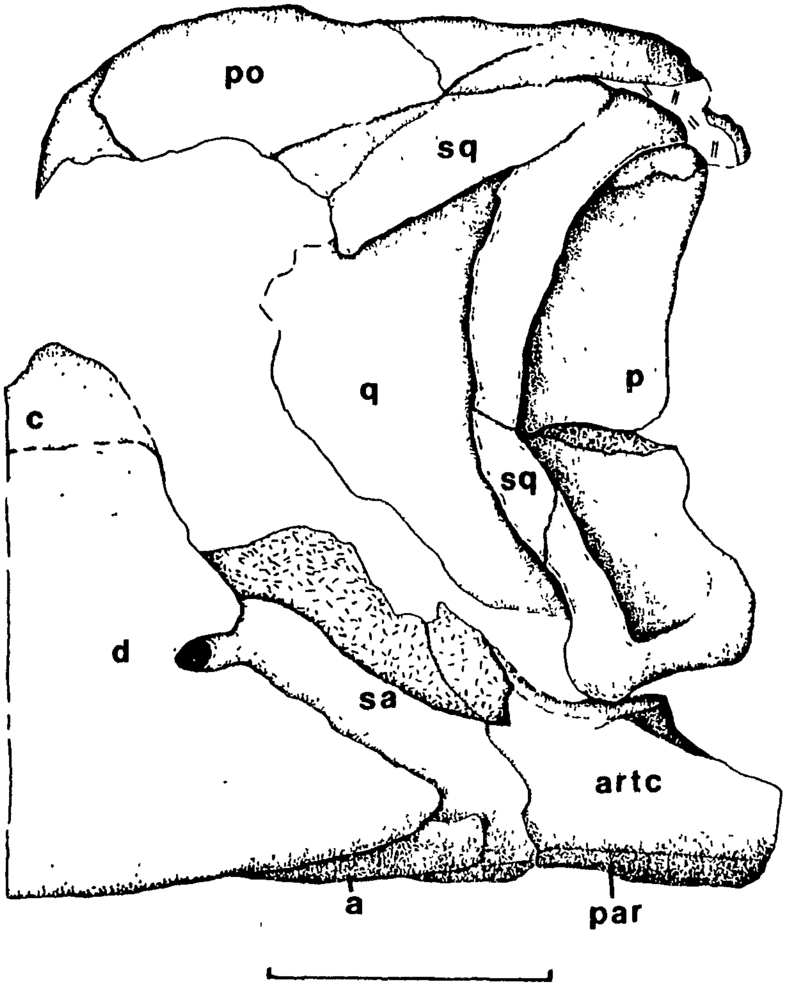
Fig. 35. *Dianosaurus petilus*. Temporal region of the skull in lateral view. Scale 5.0 mm.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posteroventral margin of the orbit. Its dorsal process is not broad at its extremity as is that of Asiacephalosaurus, but extends posteriorly to meet the squamosal before the midpoint of the supratemporal bar as in Rarojugalosaurus. The maxilla is similar to that of Sphenodon in having a dorsal edge that runs upwards along the posteroventral margin of the orbit.

c. **Palatoquadrate** (Figs. 35 and 36)

The quadrate resembles that of Rarojugalosaurus and most of sphenodontidans in that its convex cephalic head is capped by the squamosal. Poor preservation obscures its relationships to the adjacent elements. On the left side the suture between the quadrate and the quadratojugal is distinguishable below the quadratojugal foramen.

The epipterygoid is not preserved.

d. **Dermal bones of the palate** (Figs. 36--38)

The palate is generally comparable to that of Asiacephalosaurus except that the central region of the pterygoid between the three rami is not elongate. In the latter aspect, Dianosaurus resembles Rarojugalosaurus and Clevosaurus.

Fig. 36. *Dianosaurus petilus*. Occipital view of the skull. Scale bar 5.0 mm.

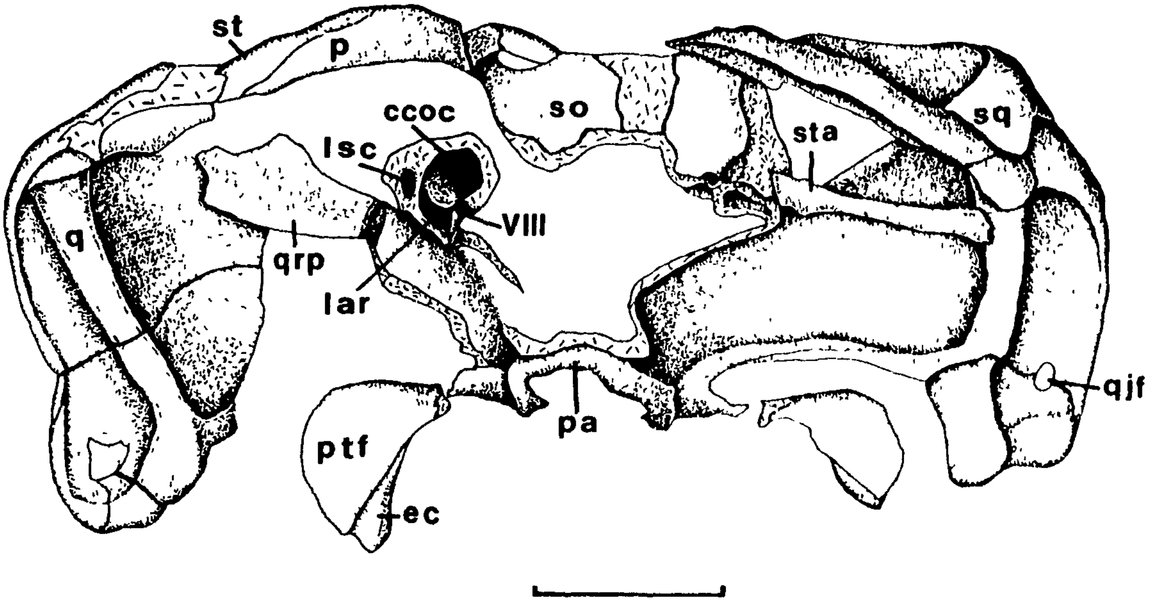
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Fig. 37. Dianosaurus petilus. Ventral view of the skull. Scale bar 5.0 mm.

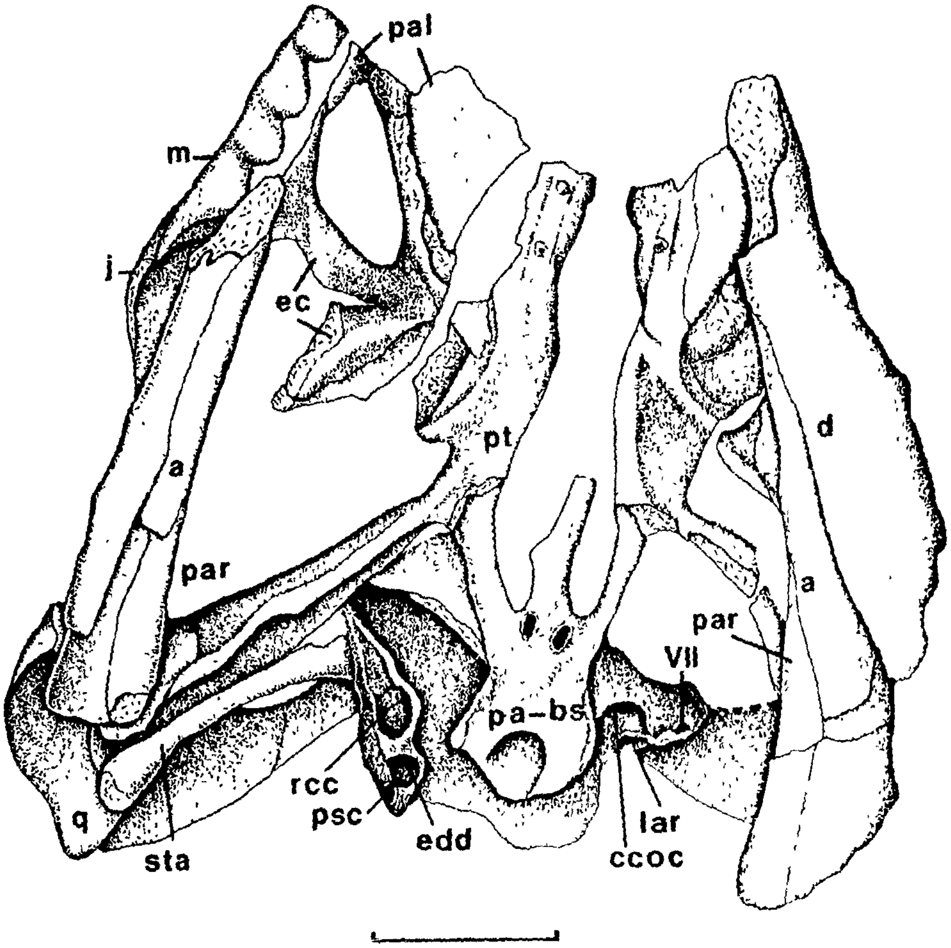
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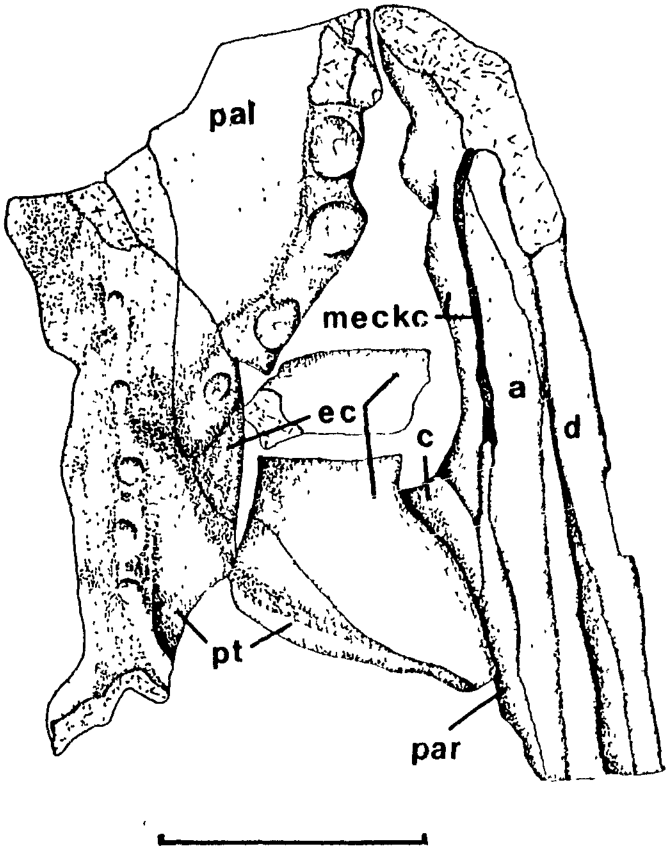
Fig. 38. *Dianosaurus petilus*. Suborbital region of the skull (with part of the left mandible) in ventral view. Scale bar 5.0 mm.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e. Braincase (Figs. 33, 36 and 37)

Of the braincase elements, only the parabasisphenoid, supraoccipital and the prootic are represented. Although incomplete, the parabasisphenoid clearly differs from that of Asiacephalosaurus, Rarojugalosaurus and other genera. It is characterized by a pair of extremely long and slender basipterygoid processes. On the ventral surface of the complex a semicircular depression is present as in Asiacephalosaurus. The preserved part of the supraoccipital does not show any difference from that of the other two Lufeng genera but some internal structures of the inner ear (unexposed in the other two Lufeng genera) are exposed on the broken surface. These structures are recognized as the foramina for the openings of the posterior semicircular canal and the endolymphatic duct and the recess crus commune with which both vertical semicircular canals connect. The preserved part of the left prootic is the portion that forms the anteroventral third of the otic capsule. On its transversely broken surface, the opening of the lateral semicircular canal, the central cavum capsularis, the lagenar recess and the foramen for one of the branches of cranial nerve VIII are well exposed. In addition, the foramen for cranial nerve VII can be identified in lateral aspect.

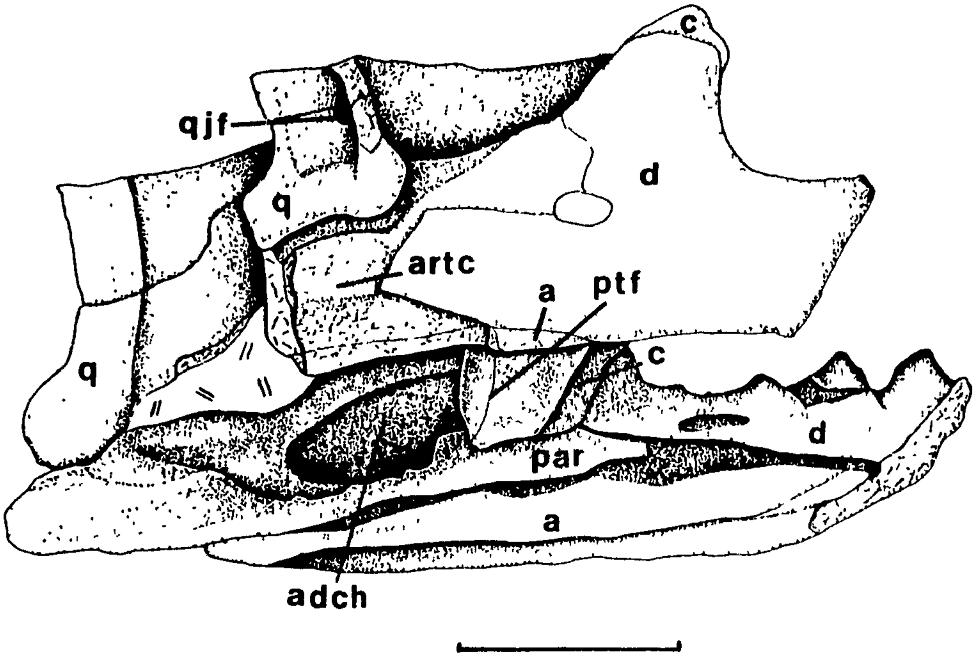
f. Mandible (Figs. 34, 35 and 37--39)

The mandible of *Dianosaurus* can be distinguished from that of the other two Lufeng genera in that the prearticular extends forwards beyond the ventral edge of the coronoid so that the latter is prevented from contacting the angular ventrally. Among sphenodontidans, this has been illustrated only for *Gephyrosaurus* by Evans (Figs. 39 and 40, 1980) although she did not mentioned it in her description. As in *Rarojugalosaurus* and most other genera, the dentary has a gently tapered posterior process.

g. Dentition (Figs. 33, 37 and 39)

The right maxilla bears the posteriormost four acrodont teeth that are of almost same size and shape. Their posterior flanges are not as conspicuous as those in *Asiacephalosaurus* and *Rarojugalosaurus*. This could be attributed to poor preservation. The anterior flanges of the three teeth of the left dentary are no more pronounced than the posterior in contrast to the condition in the other two Lufeng genera.

Fig. 39. Dianosaurus petilus. Lateral (slightly ventral) view of the skull, showing the medial aspect of the left mandible. Scale bar 5.0 mm.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SPECIMEN REFERRED TO Homoeosaurus maximiliani Meyer, 1845

Homoeosaurus was the most common genus during the Late Jurassic-Early Cretaceous period (Cocude-Michel, 1963; Fabre, 1981). Since there is no fossil record of the Sphenodontida in the Middle Jurassic and the Post-Late Cretaceous, it provides an important temporal intermediate between the Early Mesozoic genera and the living Sphenodon. Although this genus has been known for nearly 150 years, our knowledge of its cranial anatomy is still incomplete.

Many specimens of Homoeosaurus have been described, but much of their anatomy was obscured by surface erosion or crystallization of bone. This has led to incomplete and even contradictory descriptions of the same specimens, for example, between Cocude-Michel's, (1963) and Fabre's, (1981) studies (see below). One almost complete skeleton belonging to the type species H. maximiliani (C.M.6438) has been prepared by exposing the skull roof for the first time. This specimen will permit inconsistencies in previous descriptions of this species by Cocude-Michel and Faber to be resolved and provide a base for establishing the phylogenetic relationship of the genus, Homoeosaurus, thus allowing an assessment of the significance of the genus in the evolution of the Sphenodontida.

Historical Background of the Specimen

Specimen C.M.6438, which is here referred to as Homoeosaurus maximiliani, is an undescribed skeleton originally exposed in ventral view. It was collected by C. Bayet in 1903 from the Upper Jurassic Solnhofen Limestone at Solnhofen, Germany and was initially referred to as Homoeosaurus macrodactylus, established by Wagner in 1852. More than one hundred years later H. macrodactylus was placed by Kuhn (1961) in the Iguania and more recent by Hoffstetter (1964) and Estes (1983) to the Gekkota under the name of Bavarisaurus macrodactylus. However, an acrodont dentition, the absence of the lacrimal, the contribution of the postfrontal to the supratemporal fenestra, the elongated posterior process and the large dorsal coronoid projection of the dentary, and a lateral row of large palatine teeth clearly indicate that this specimen represents a sphenodontidan lepidosaurian. It can be attributed to the genus Homoeosaurus on the basis of small supratemporal fenestrae, a broad parietal table and long limbs (Cocude-Michel, 1963; Fabre, 1981).

As part of a revision of Homoeosaurus, Cocude-Michel (1963) verified three species within the genus based primarily on the proportions of the postcranial skeleton. They are H. maximiliani, H. solnhofen and H. parvipes (=Lepidosaurus neptunius, Fabre, 1981). According to the proportions of the humerus, radius, femur and tibia to the presacral vertebrae

(Table 1), C.M.6438 can be referred to the species H. maximiliani. This assignment is further demonstrated by the fact that the complete rear limb is longer than the entire presacral vertebral column (Fig. 40).

Description

The specimen is an almost complete skeleton with a total length of about 17 cm. The skull is approximately 1.7 cm long. The limb bones in certain regions were damaged. The ventral aspects of the skull and both shoulder and pelvic girdles have been heavily eroded. The vertebral column is still articulated. The crystallization of the surface of the specimen makes it difficult to examine sutures between elements in some areas. The dorsal elements of the skull are well-preserved.

a. Dermal bones of the skull roof (Figs. 41--46)

The left premaxilla is almost complete. In contrast with the reconstructions of Cocude-Michel (1963) and Fabre (1981), the bone has no pronounced nasal process dorsally, and forms only the anterior and anterolateral third of the margin of the external naris.

The right maxilla is well-preserved, but its anterodorsal part is still covered by matrix. The extremely broad dorsal process extensively overlaps the prefrontal and nasal, and

Table 1. Body Proportions of the Three Species of Homoeosaurus and C.M. 6438

	H/PSVC	R/PSVC	F/PSVC	T/PSVC
H. maximiliani*	0.27	0.21	0.35	0.32
C.M. 6438	0.25	0.21	0.34	0.33
H. solnhofensis (R.4073)	0.24	0.17	0.30	0.26
H. parvipes (Rhy.1)	0.18	0.14	0.25	0.20

Note: H--Humerus; PSVC--Length of the presacral vertebrate column; R--Radius; F--Femur; T--Tibia; *--Average of eight specimens; R.4073--A specimen of Museum Senckenberg; Rhy.1--A specimen of the geological laboratory, University of Berlin. The data are from Cocude-Michel (1963) except for C.M. 6438.

Fig. 40. _Homoeosaurus_ _maximiliani_. Skeleton of C.M. 6438 in ventral view. Scale bar 10. mm.

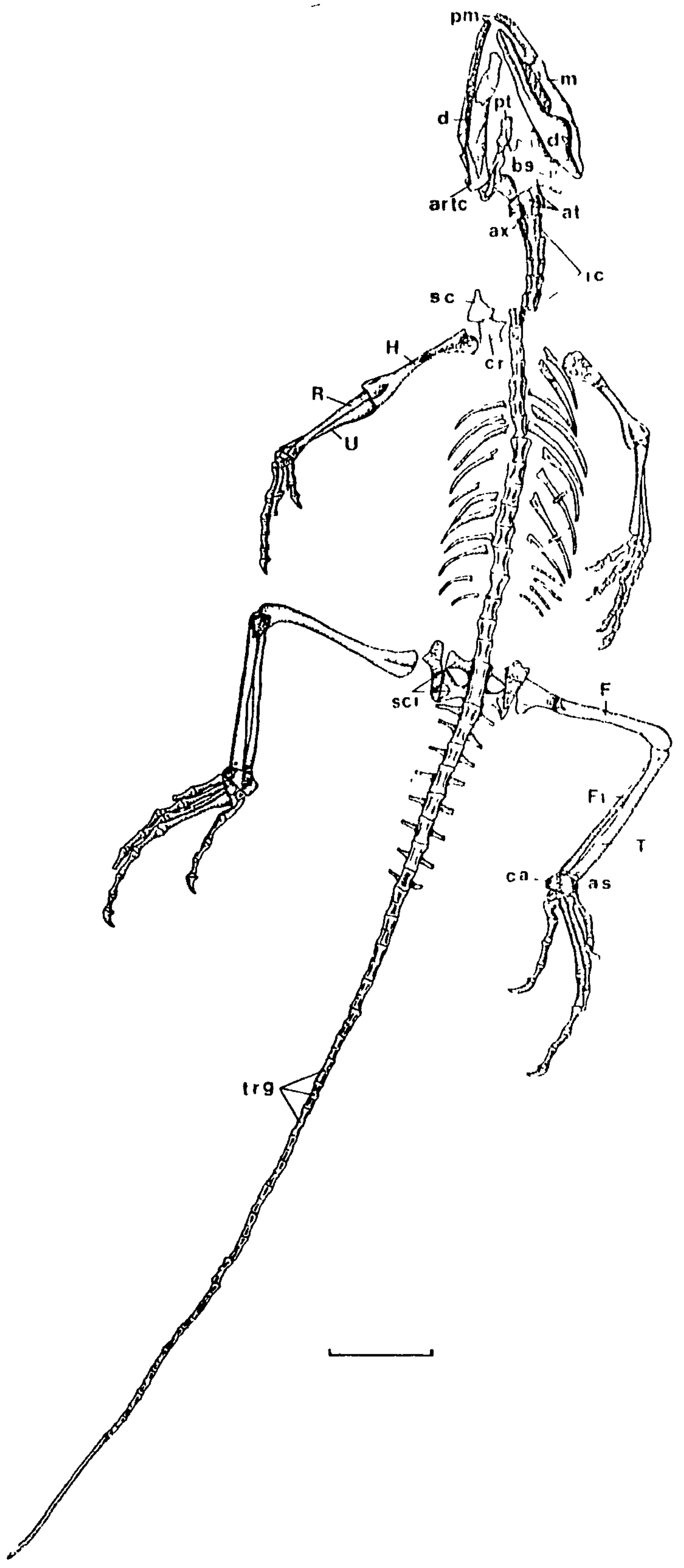
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Fig. 41. _Homoeosaurus_ _maximiliani_. Dorsal view of the skull of C.M. 6438. Scale bar 5.0 mm.

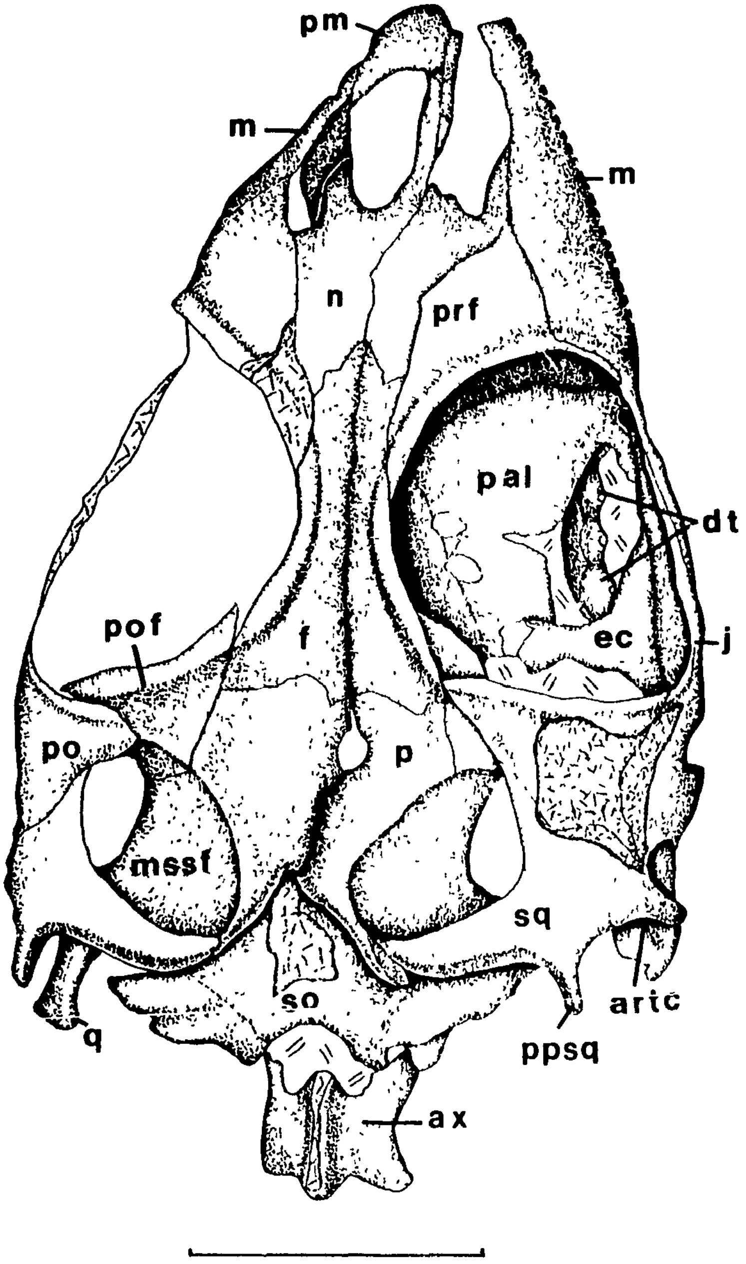
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Fig. 42. _Homoeosaurus_ _maximiliani_. Reconstruction of the skull of C.M. 6438 in dorsal view. Scale bar 5.0 mm.

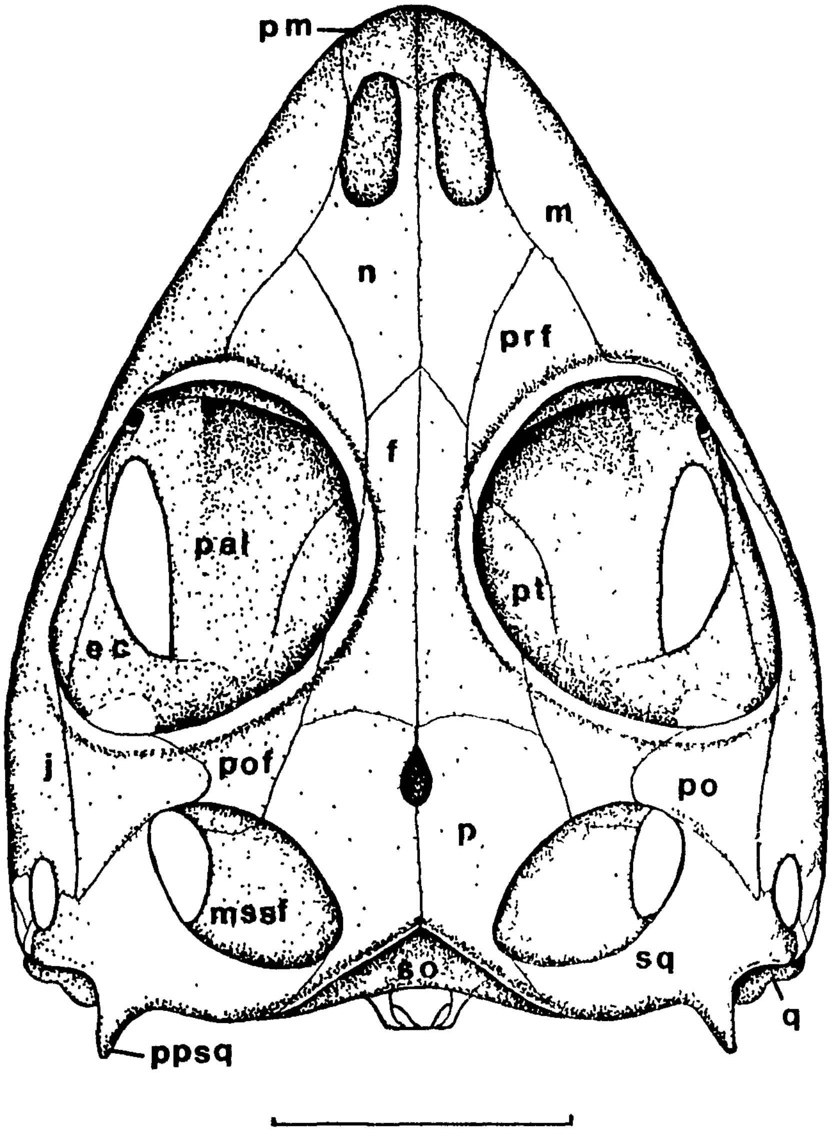
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Fig. 43. <u>Homoeosaurus</u> <u>maximiliani</u>. Lateral view of the skull of C.M. 6438. Scale bar 5.0 mm.

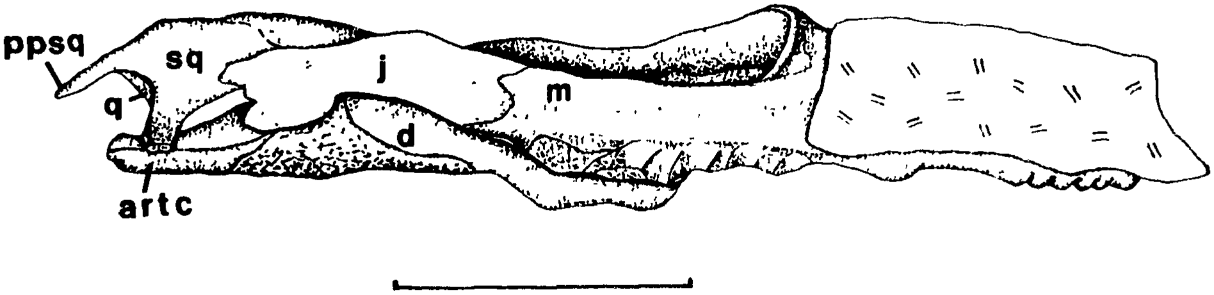
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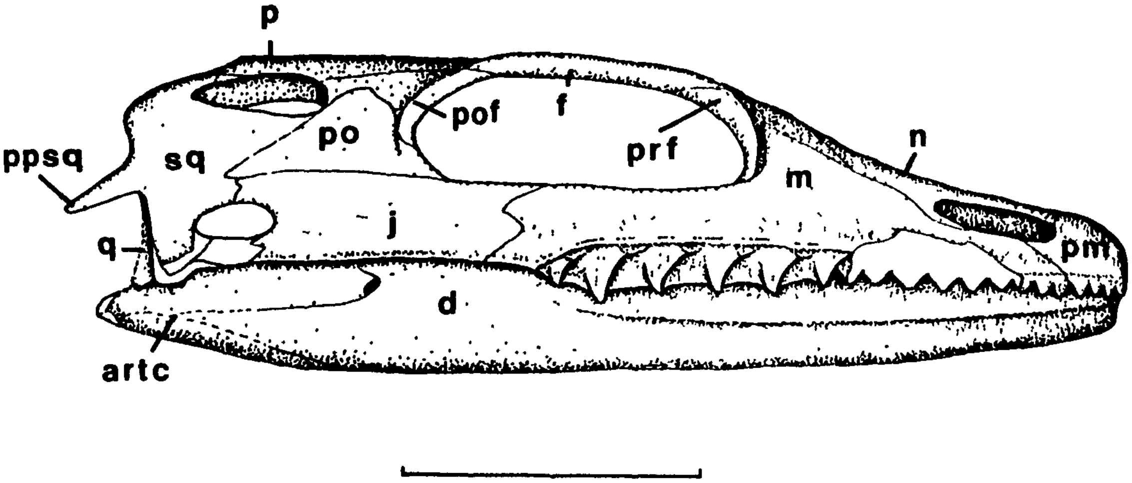
Fig. 44. Homoeosaurus maximiliani. Reconstruction of the skull of C.M. 6438 in lateral view. Scale bar 5.0 mm.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anteriorly overlaps the premaxilla. It forms only the middle -third of the lateral margin of the external naris rather than the entire lateral border as reconstructed by Cocude-Michel (1963) and Fabre (1981). The forked posterior process is not sharply pointed. Medially, the maxilla has a broad contact with the jugal and a much more restricted contact with the maxillary process of the palatine at the anteroventral corner of the orbit. This configuration is distinct from the two previous reconstructions in that the maxilla does not extend along the whole ventral margin of the orbit. As in other sphenodontidans, the maxilla extends laterally posterior to the tooth row around the adductor chamber.

Both nasals are nearly complete and their sutures with adjacent bones are clearly marked. The most significant difference from previous reconstructions is the presence of very slender anterior processes that form the entire internarial septum. As in many other sphenodontidans, the suture between the nasals and the frontals is V-shaped. Anterior to the suture the nasals show a sharp curvature, facing anterodorsally and then forming a quite flattened snout region.

As noted in previous reconstructions, the external nares are considerably larger than those of other sphenodontidans, with a very narrow interseptum.

The well preserved right prefrontal shows a very limited lateral exposure of its ventral process as in Sphenodon and Palaeopleurosaurus. Its dorsal portion is more widely exposed than was indicated by the previous reconstructions. The suture between the prefrontal and the palatine is visible through the orbit. The lacrimal is absent, but no lacrimal foramen is exposed on the lateral surface.

The frontals are paired and complete, but the right is a bit obscured posteriorly by the displacement of the left. Each bears a lateral ridge, not indicated in previous descriptions, that continues onto the neighbouring bones around the orbit. Medial to the ridge the bone is concave along the midline. Sutures are clearly visible between the frontal and adjacent bones.

The relationships of the paired parietals with the neighbouring bones are clearly marked in C.M. 6438, although the left one is slightly displaced to the right posteriorly. In contrast with previous reconstructions, the very small supratemporal fenestra is more oval in shape with a long axis set oblique rather than parallel to the sagittal plane. The structure of the relatively narrow parietal table, more or less goblet-shaped, does not confirm to previous accounts. The ratio of the parietal table/interorbital width is about 1.3 in this specimen as compared to around 2.0 in the previous reconstructions. The most significant difference is that the parietal has a large laterally expanded portion that slopes away from the margin of the parietal table and forms a broad medial shelf of the supratemporal fenestra for the attachment of adductor muscles. The supratemporal passage occupies only the lateral third of the fenestra so that the parietal region

Fig. 45. Homoeosaurus maximiliani. Ventral view of the skull of C.M. 6438. Scale bar 5.0 mm.

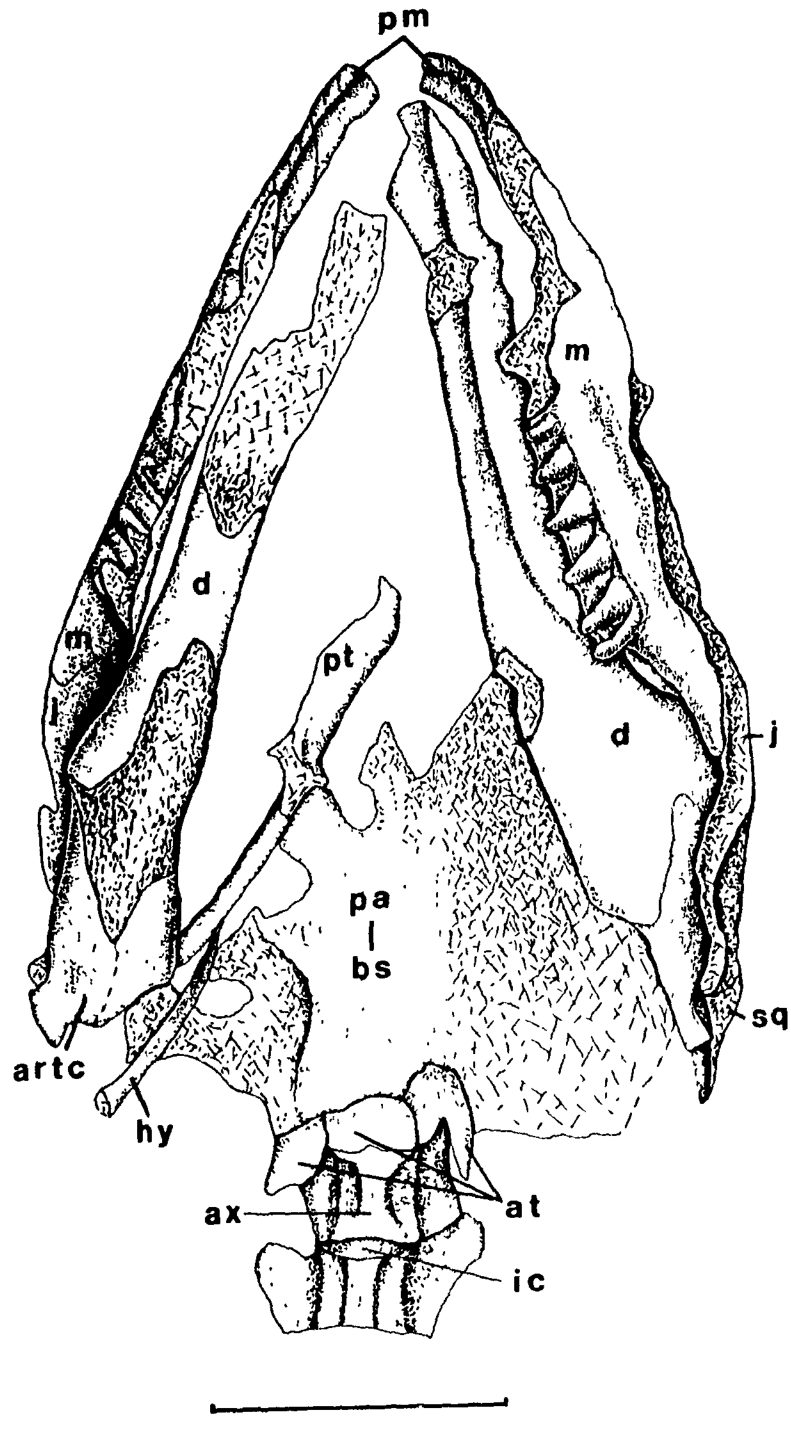
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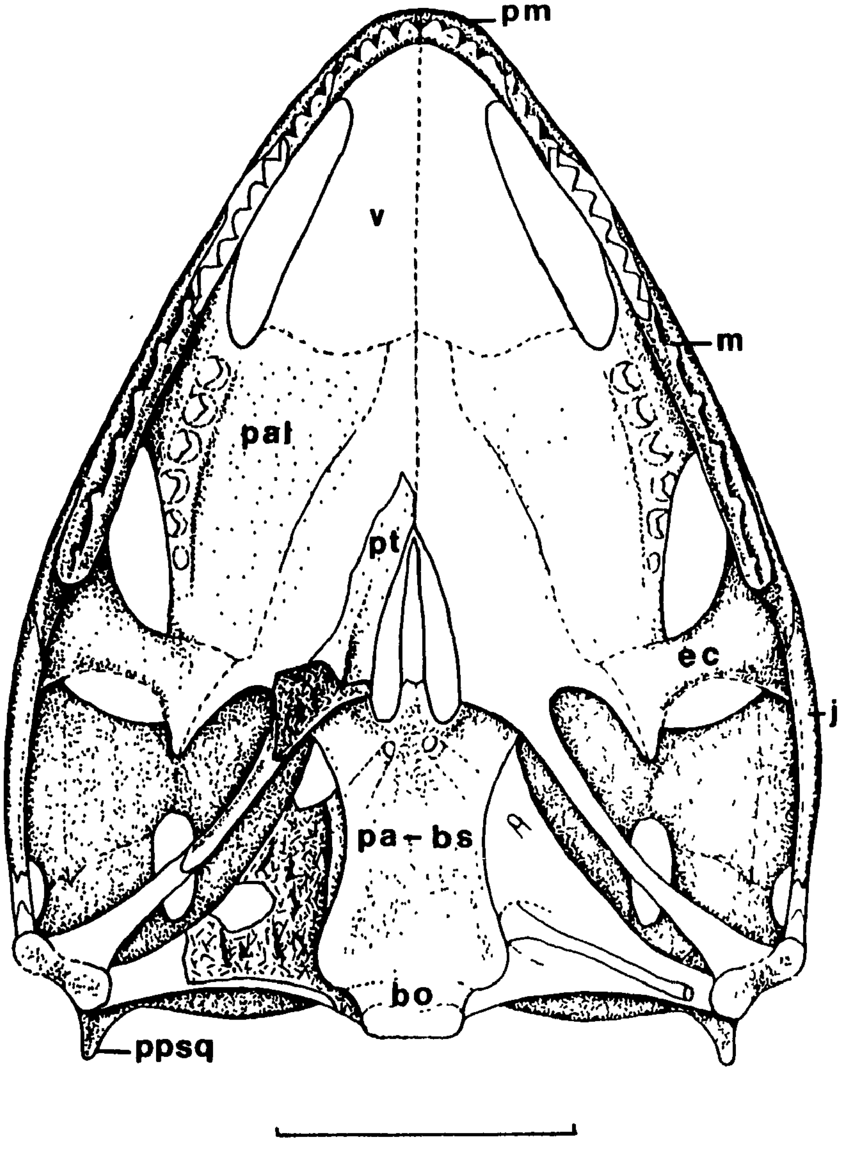
Fig. 46. Homoeosaurus maximiliani. Reconstruction of the skull of C.M. 6438 in ventral view. Scale bar 5.0 mm.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between the supratemporal passages is about three and half times as broad as the interorbital width. The posterior margin of the parietals is V-shaped, rather than slightly curved. As in Sphenodon, a posterolateral process of the bone appears as a thin, nearly vertical structure that is extensively overlapped laterally by the squamosal. The parietal foramen is located just anterior to a line drawn between the anterior borders of the supratemporal fenestrae, and its anterior margin almost reaches the suture between the parietals and the frontals.

The postfrontal is fully exposed on the left side. It is distinct in two aspects: medially, it has a more extensive contact with the parietal than with the frontal, and posteriorly, it makes a modest contribution to the medial shelf of the supratemporal fenestra.

The left postorbital shows clear relationships with the postfrontal and the squamosal dorsally while the right displays its suture to the jugal ventrally. In its triangular configuration and sutural pattern with adjacent bones, it resembles that of other sphenodontidans, although its contribution to the anterior margin of the supratemporal fenestra is more restricted.

The right jugal is complete except for the end of the posterior process. Contrary to previous reconstructions, it is narrow and strap-shaped, without the typical dorsal process of other sphenodontidans, and has two posterior processes above and below the inferior temporal fenestra. The lower process, which forms the lower temporal bar, probably extended backwards to contact the squamosal and quadratojugal although it is damaged; the upper process meets the squamosal and separates the postorbital from the lower temporal fenestra. The anterior process of the jugal is longer than previously thought, and it meets the infraorbital foramen anteriorly. The suture with the ectopterygoid is well exposed through the right orbit.

Although damaged at its ventral extremity, the right squamosal is almost complete, permitting a description of its relationships with adjacent bones for the first time. Although it shows a generally similar configuration to that of other sphenodontidans, the bone is very peculiar in having a remarkably pronounced posterior process that forms a notch-like structure on the posterolateral side of the skull that probably served as a support for the attachment of the dorsal margin of the tympanum. Its medial process is relatively extensive in comparison with that of other sphenodontidans. Its posterior margin turns down to form a surface that extends laterally to the posterior process and serves for the attachment of the M. depressor mandibulae. Its anterior process is very broad and forms, together with the postorbital and the jugal, a wide supratemporal bar. Its descending process runs ventrally without tapering. The inferior temporal fenestra is much smaller than the supratemporal fenestra, and even smaller than the opening of the external naris. It is an elongated oval parallel to the upper jaw although its lower margin is not complete in the specimen at hand.

The supratemporal is not formed.

b. Palatoquadrate (Figs. 41)

No bones of the palatoquadrate have previously been described in Homoeosaurus. In C.M.6438, the left quadrate is preserved, showing a column-like shape as in chamaeleontid lizards, although this may be an artifact of preservation. It is impossible to establish the exact configuration of the bone or its relationship with the quadratojugal.

The epipterygoid is not exposed.

c. Dermal bones of the palate (Figs. 41, 42, 45 and 46)

Among the components of the palate, only the pterygoid was described by Cocude-Michel (1963). In C.M.6438, the palatine, pterygoid and ectopterygoid are exposed to a variable extent. The right palatine is nearly completely exposed through the orbit. The maxillary process does not meet the ectopterygoid posteriorly along the lateral margin of the suborbital fenestra. The maxilla and the jugal form the lateral border of the infraorbital foramen. Anteriorly, the palatine receives the ventral process of the prefrontal. Medially, parts of its suture with the pterygoid are visible. Posteriorly, its width is reduced but it is not tapered. The ventral surface of the palatine is obscured by surface crystallization.

The fragment of the right pterygoid of C.M.6438 displays a short central region as in most early genera. No teeth are visible on the ventral surface of the preserved portion.

The ectopterygoid is displayed dorsally through the right orbit. Its lateral process is complete and attaches to the jugal dorsally and probably to the maxilla ventrally as in other lepidosaurs. It is clear that the medial process makes contact with the palatine at the posteromedial corner of the suborbital fenestra, which separates the pterygoid from the fenestra as in many other sphenodontidans. The relationship with the pterygoid flange cannot be established because of poor preservation.

d. Braincase (Figs. 41, 45 and 46)

No description of the braincase was made in previous studies. In this specimen, the braincase is also poorly preserved and further obscured by the crystallization of calcite on the surface of the bones. Little other than the total length of the braincase floor can be established. The right basipterygoid process is relatively robust. In occipital view the dorsal margin of the foramen magnum is complete, and the otic capsule seems quite large.

On the left side of the palate, a rod-like bone is probably a fragment of the hyoid apparatus.

e. Mandible (Figs. 43, 44 and 45)

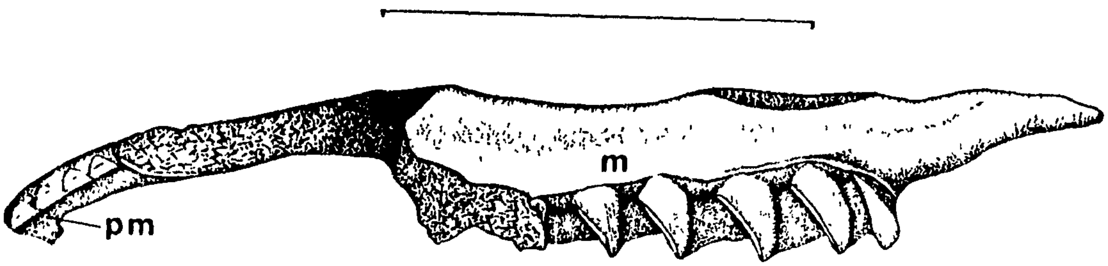
Little can be added to Cocude-Michel's description of the mandibles from C.M.6438. Both mandibles are present, but only the dentary is well-preserved. The bone shows a elongated posterior process and a large dorsal coronoid projection as in other sphenodontidans. Although the posterior part of the mandible is obscured by the crystallization, the retroarticular process is clearly not as pronounced as that of the earlier sphenodontidans. It may have been reduced as in Sphenodon. In Cocude-Michel's reconstruction of the mandible, the process is evidently short.

f. Dentition (Figs. 41, 44--47)

In a detailed description of the dentition of Homoeosaurus, Cocude-Michel (1963) hypothesized that there were two premaxillary teeth on each side in juvenile individuals and that they were worn down to become a single cutting edge in mature individuals as in Sphenodon. C.M.6438 clearly shows four teeth in the left premaxilla and three in the fragment of the right, which implies that the specimen was not a fully mature individual. The four small premaxillary teeth are similar in size and conical in shape. Although the specimen is immature, the teeth clearly show the presence of worn surfaces on the lingual side.

The last five teeth of the left maxilla are complete. The

Fig. 47. Homoeosaurus maximiliani. Dentition of the left upper jaw of C.M. 6438. Scale bar 5.0 mm.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most posterior one is much smaller than the others and is not fully ankylosed with the dentary. The remainder decrease in size anteriorly but are similar in configuration. Contrary to previous descriptions, these teeth show very sharp anterior edges. These teeth occupy about one half the length of the maxilla. The anterior maxillary teeth on the right side display a similar size and configuration to those of the premaxilla.

Three dentary teeth are exposed through the right suborbital fenestra. They are conical and enlarged in size posteriorly. As in many other sphenodontidans, they have a pronounced anterior flange.

g. Postcranial skeleton (Figs. 40, 41, 45, 48 and 49)

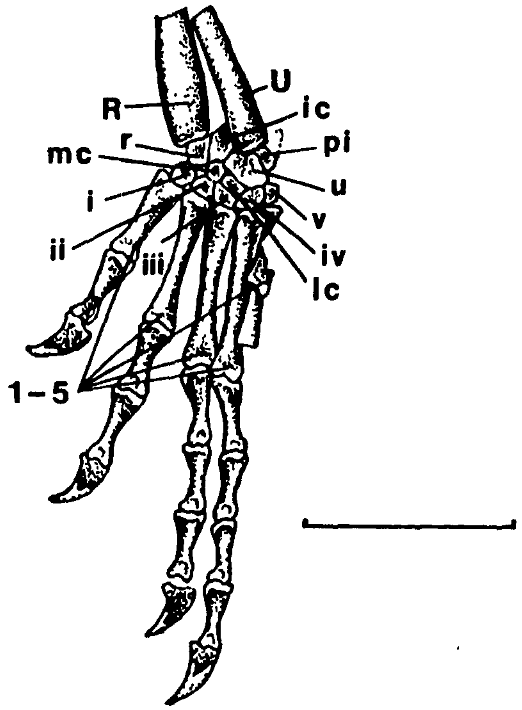
Although most of the postcranial skeleton of H. maximiliani was adequately described by Cocude-Michel (1963) and Fabre (1981), this specimen can further clarify the following aspects.

Of 24 presacral vertebrae, only the cervicals have intercentra. The second sacral rib is forked laterally. Following the 30th caudal vertebra is a 16 mm long bony extension that is most probably formed by the fusion of the rest of the caudals. Beyond the seventh or the eighth caudal, the vertebrae show the capacity for caudal autonomy, demonstrated by a transverse groove at the midpoint of the centra.

All elements of the left carpus are preserved. Although slightly displaced, their arrangement resembles that in Sphenodon. However, unlike Sphenodon, the medial centrale is smaller than the lateral centrale, and the fourth metacarpal is the longest one, as described by Cocude-Michel (1963). In this aspect Homoeosaurus is comparable to Pleurosaurus goldfussi (Cocude-Michel, 1963) and to Polysphenodon (Carroll, 1985; Fraser and Benton, 1989). In other sphenodontidans, the third metacarpal is the longest.

Other sphenodontidans in which the tarsus is preserved all show the fibula articulating with a facet that extends across the suture between the calcaneum and the astragalus, or across the line marking the boundary between the two elements. As in Cocude-Michel's reconstructions, the calcaneum and the larger astragalus of C.M. 6438 are suturally attached, and the tibia and fibula both articulate solely with the astragalus. Despite the presence of a distinct fibular facet on the calcaneum of C.M. 6438 and most specimens, why do most specimens of Homoeosaurus show the fibula very close to the tibia and sharing with it the same articular surface on the astragalus? The answer is probably associated with the displacement of the fibula relative to the tibia. Muscles such as the M. interosseous and the M. popliteus and tendons between the two elements presumably pulled the lighter fibula out of its articular facet to bring it close to the more massive tibia when they became dry before burial. If this were true, then the ankle joint of Homoeosaurus was wrongly

Fig. 48. Homoeosaurus maximiliani. Left hand of C.M. 6438 in anterior view. Right, reconstruction of the hand. Scale bar 5.0 mm.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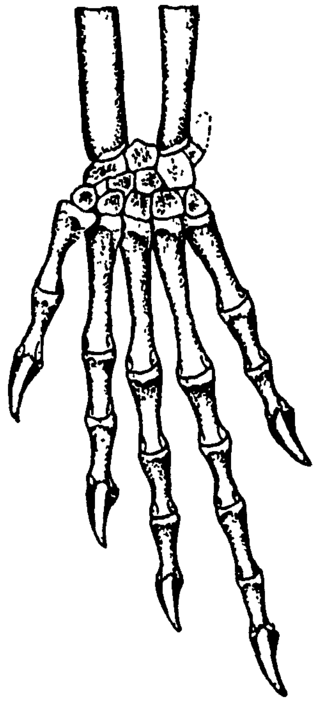
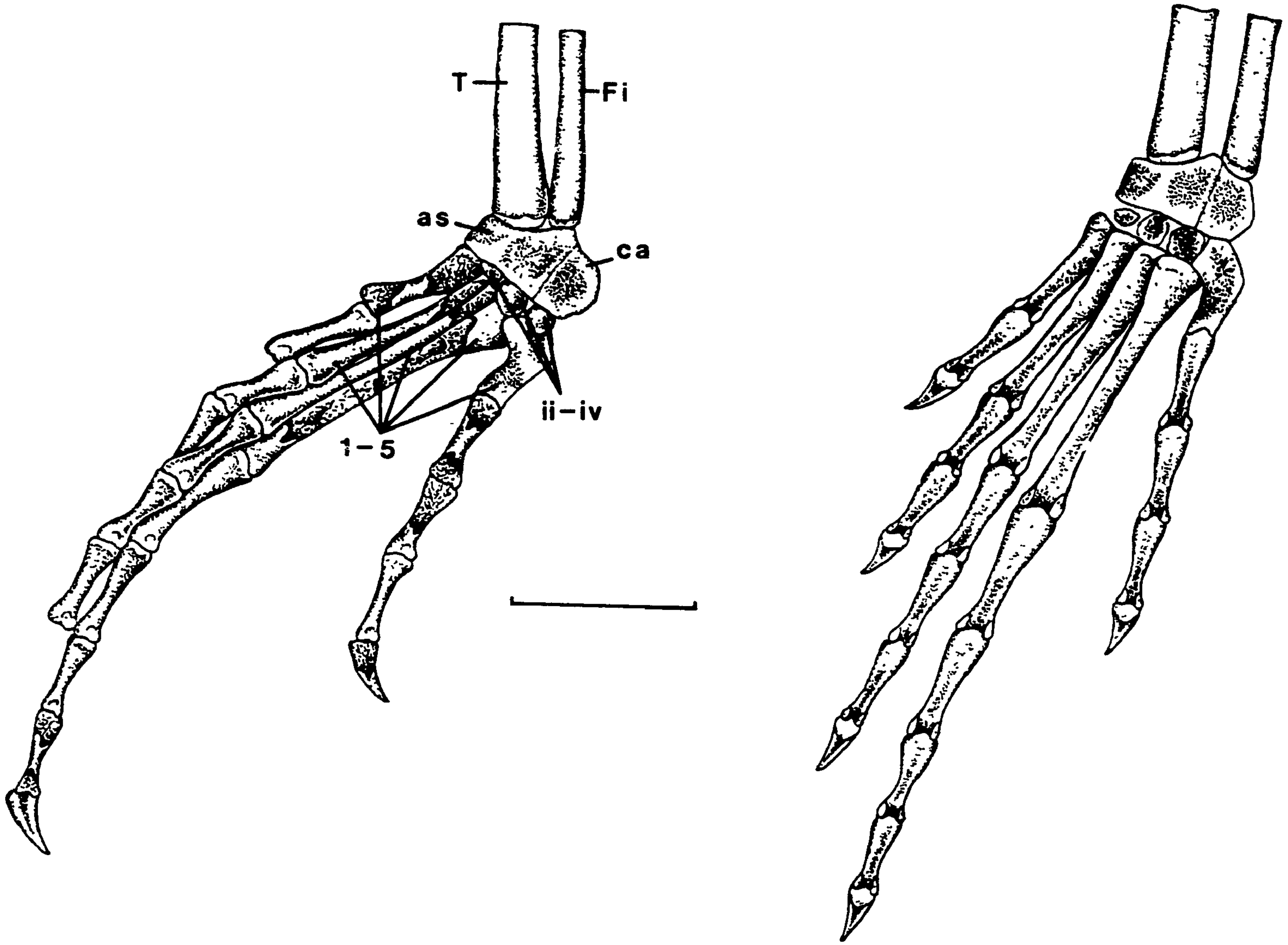


Fig. 49. <u>Homoeosaurus</u> <u>maximiliani</u>. Right foot of C.M. 6438 in posterior view. Right, reconstruction of the foot. Scale bar 5.0 mm.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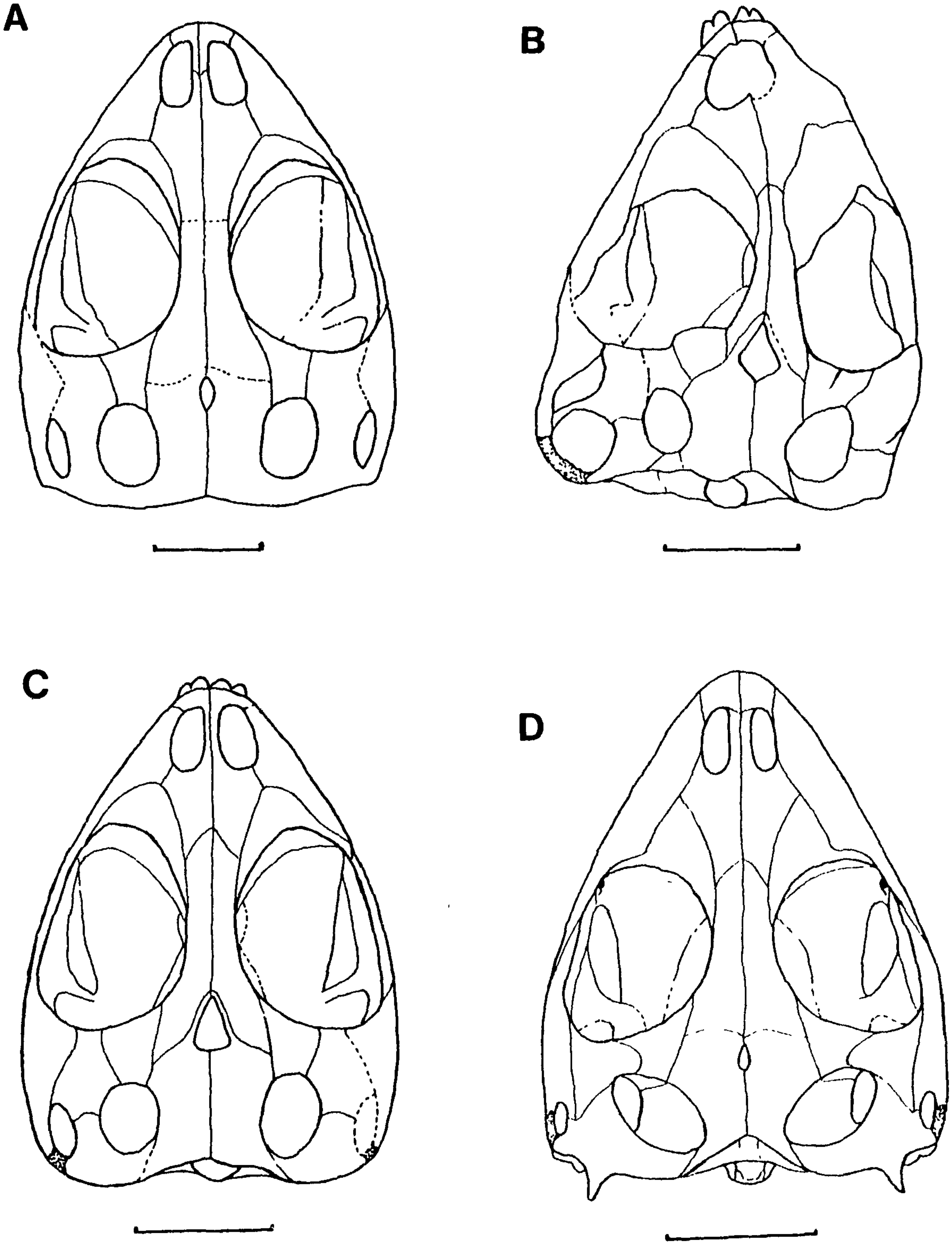
restored in Cocude-Michel's paper (1963). In C.M. 6438, distal tarsals 2--4 are also out of their original position on both sides. Their improper articulation with the metatarsals must have been caused by the contraction of the flexor group of muscles or tendons when air-dried.

Reconstruction of the Skull

Cocude-Michel (1963) and Fabre (1981) reconstructed the skull of H. maximiliani in dorsal view (Fig. 50 A and C). Fabre's reconstruction, based on one of his paratypes (No. 1930-I-40, Munich), differs slightly from that of the holotype (Cocude-Michel, 1963). Fabre restored the skull with a relative large, pear-shaped and anteriorly positioned parietal foramen.

I have restored the skull in three views (Figs. 42, 44, 46 and 50D). C.M. 6438 indicates that the skull of H. maximiliani differs from previous reconstructions in the following ways: the postorbital region is a bit broader, while the snout is slightly longer; the orbits are relatively small, about one-thirds of the total skull length, and almost as long as the snout; the dorsal process of the maxilla is wider and deeper posteriorly, resulting in a very limited lateral exposure of the prefrontal anterior to the orbit; the septum between the external nares is formed entirely by the nasal bones; and the postorbital are generally broadly triangular as in other sphenodontidans and has similar sutural

Fig. 50 Homoeosaurus maximiliani. Dorsal views of the skulls. A, reconstruction of the type skull, (after Cocude-Michel, 1963). B, skull of paratype 1937-I-40 and C, reconstruction of the skull of 1937-I-40, (after Fabre, 1981). D, reconstruction of the skull of C.M. 6438. Scale bars 5.0 mm.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patterns with the adjacent bones. Since the anatomy of the jugal, squamosal and parietal were not well known in the two previous studies, the most significant differences between the two previous reconstructions and mine are concentrated in the temporal region and the parietal area. My restoration of a pronounced posterior process of the squamosal, a strap-shaped jugal, a relatively narrow and goblet-shaped parietal table, a wide medial shelf of the supratemporal fenestra, a broad parietal region between the supratemporal passages, and a pair of peculiarly small inferior temporal fenestrae are indisputable. In addition, the considerably curved posterior margin of the skull and a long-oval suborbital fenestra are also clearly marked in C.M. 6438. The size and the position of the parietal foramen indicated by the new material are comparable to that displayed by Cocude-Michel's reconstruction (1963). Although C.M. 6438 is not a fully mature individual, these reconstructions of the skull should be reliable except for the palate region and the otic capsule that have been based on very fragmental remains. A slender stapes is entirely copied from that of Asiacephalosaurus.

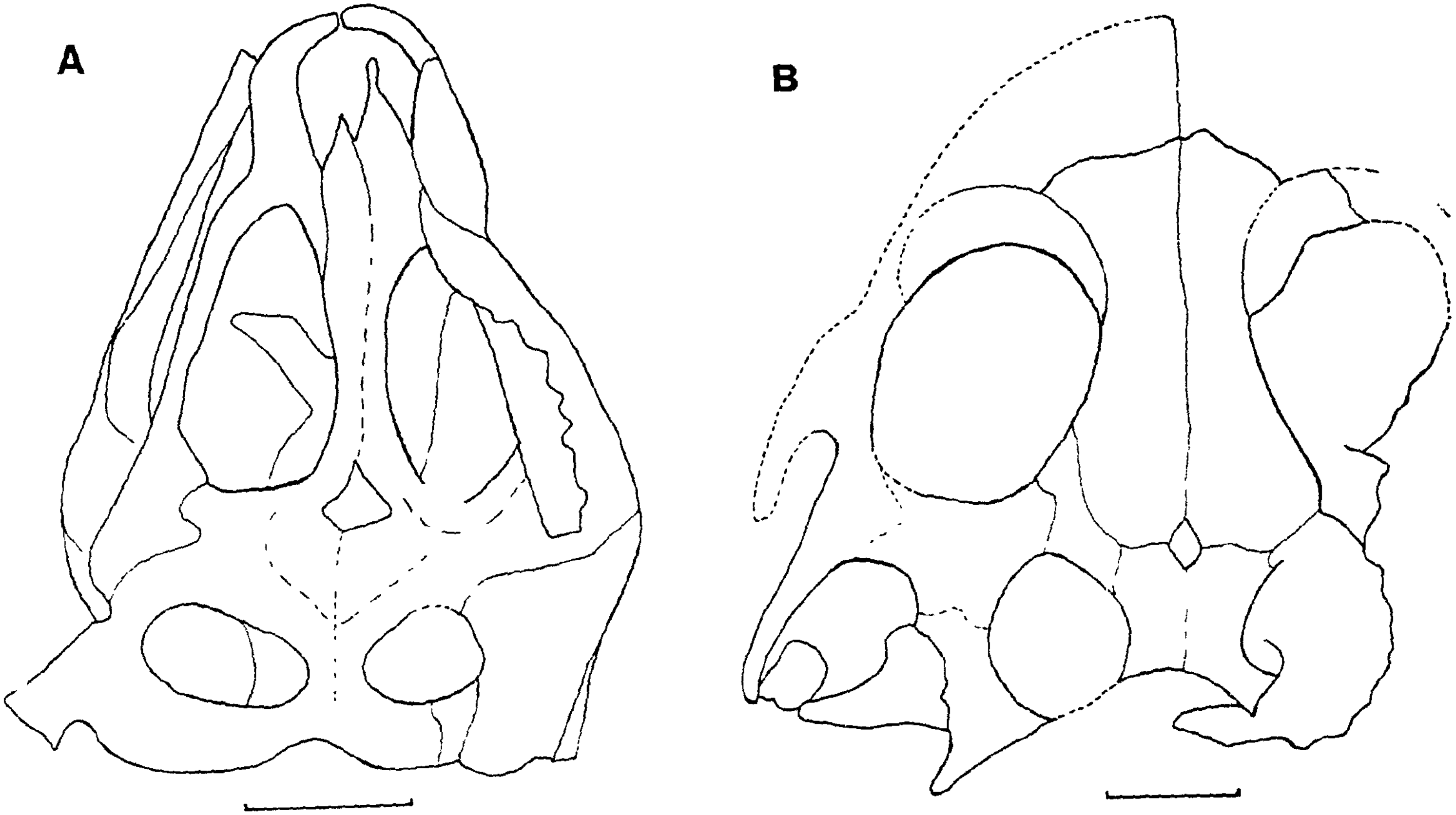
Assessment of the Principal Differences Between C.M. 6438 and Previously Studied Specimens

No significant differences of the postcranial skeleton were noticed between C.M. 6438 and previously studied specimens of H. maximiliani. However, C.M. 6438 shows several previously unknown cranial features of <u>Homoeosaurus</u> that are unique within the Sphenodontida. These include the very pronounced posterior process of the squamosal forming a notch -like structure on the posterolateral side of the skull, the anterolaterally-posteromedially oriented supratemporal fenestra leading to a goblet-shaped parietal table, the very broad medial shelf of the supratemporal fenestra forming a very wide parietal region between the supratemporal passages, and the strap-shaped jugal.

The pronounced posterior process of the squamosal and the medial shelf of the supratemporal fenestra were illustrated in Fabre's paper (1981). Although he did not mention these features in his study, his figure 13 of a line-drawing of the skeleton of the neotype (specimen ASI 565, Institute of Paleontology, Munich) shows that the medial shelf is present in the left supratemporal fenestra and that the left squamosal displays a posterior extension that was a bit damaged at the extremity (Fig. 51A). The posterior process of the squamosal is also visible in his figure 21 of another skeleton of the species (Fig. 51B). The significance of the development of the process to the sphenodontidan evolution will be discussed later.

As figure 51A shows, the medial shelf of the left supratemporal fenestra in ASI 565 occupies about one-third of the fenestra rather than two-thirds as in C.M. 6438. As a result, the supratemporal passage appears very wide, but the parietal region between them is much narrower than that of

Fig. 51. Homoeosaurus maximiliani. Dorsal views of the skulls of A, neotype ASI 565 and B, specimen Col. Ghirardi (=Homoeosaurus aff. solnhofensis, Fabre, 1973) (after Fabre, 1981). Scale bars 5.0 mm.


A
B

C.M. 6438. The skull of ASI 565 is 23 mm long, which is 1.5 mm shorter than that of the largest specimen of the species (Cocude-Michel, 1963; Fabre, 1981) and 6 mm longer than that of C.M. 6438. The latter is an immature individual on the basis of the premaxillary dentition. Therefore, ASI 656 can be considered as a mature specimen. If the left supratemporal fenestra of ASI 565 shows an original configuration and there was limited individual variation within the species, then the difference in the supratemporal fenestra between ASI 565 and C.M. 6438 may have been associated with ontogenetic changes, i.e., the supratemporal fenestra has a broad medial shelf and a narrow temporal passage in younger individuals but, conversely, a narrow medial shelf and a broad temporal passage in older specimens. Such a change in relative size between the two portions of the supratemporal fenestra during growth has been well established in the Chinese crocodile, <u>Alligator sinensis</u> in which the medial shelf of the supratemporal fenestra is always reduced in older specimens and only occupies one-third of the fenestra in adults (Cong et al, 1984). The medial shelf of the supratemporal fenestra is developed to various degrees in all known sphenodontidans in which the skull is adequately preserved, but the structure never reaches 25% of the total area of the fenestra with the exception of <u>Palaeopleurosaurus</u> where the medial shelf of the supratemporal fenestra is relatively wide, occupying almost one-third of the fenestra.

Of the previously studied specimens of <u>H</u>. <u>maximiliani</u>

that are exposed in dorsal view, ASI 565 is the only specimen that shows the presence of the medial shelf of the supratemporal fenestra. It is interesting that one of Faber's paratypes (RMc 1, Jura-Museum), which is slightly smaller than C.M. 6438, did not show the medial shelf of the supratemporal fenestra to any degree.

The anterolateral-posteromedial orientation of the supratemporal fenestra can be seen in ASI 565. The parietal table in this specimen may have also been goblet-shaped as in C.M. 6438.

Because of the poor preservation of the jugal in all specimens previously studied, it cannot be demonstrated that the bone of C.M. 6438 shows the typical configuration for H. maximiliani, but it should be emphasized that the horizontal extension of the posterodorsal process above the inferior temporal fenestra is an unquestionable feature in C.M. 6438.

The phylogenetic position of the species will be discussed in a later section of this thesis.

COMPARATIVE MORPHOLOGY OF THE MIDDLE EAR REGION OF THE FOSSIL GENERA AND ITS IMPLICATIONS FOR THE AUDITORY EVOLUTION OF THE SPHENODONTIDA

Although many anatomical characters of fossil sphenodontidans have become clear in recent years, morphological studies of the middle ear region have been limited to the tympanic frame of the early genera (Robinson, 1973; Evans, 1980; Fraser, 1982; Carroll, 1985; Whiteside, 1986). Few detailed studies have been made of the middle ear apparatus of either the early or late fossil sphenodontidans. Hence it is not certain if an impedance matching middle ear sensitive to airborne sound was ever possessed by any member of the Sphenodontida. Traditional concepts of the primitive nature of the middle ear apparatus of the living genus Sphenodon have been questioned by recent work (Gans and Wever, 1976; Carroll, 1985 and 1988a; Whiteside, 1986; etc.). However, it has long been believed that the pattern of the middle ear apparatus of modern lizards is uniquely derived (see Gauthier et al., 1988), and therefore of limited value in the analysis of hearing mechanisms in the Sphenodontida. Descriptions of new genera from China and Homoeosaurus maximiliani from Europe make it possible to make a comparative study of the morphology of the middle ear apparatus of fossil sphenodontidans, forming the basis for a possible resolution to this question. A brief introduction to the structures and functions of the middle ear apparatus both of most lizards (despite their alleged derived condition) and Sphenodon will be helpful in understanding the middle ear apparatus of the fossil genera of the Sphenodontida.

A typical lizard middle ear (Wever, 1978) includes the following structures (Fig. 52): a large membraneous tympanum supported by a bony frame formed by the lateral rim of a basin-like conch on the lateral surface of the quadrate and the retroarticular process of the lower jaw; a hollow air-filled chamber positioned lateral to the braincase; two windows, the fenestra ovalis and the fenestra rotundum, located on the lateral wall of the braincase and a slender stapes between the tympanum and the fenestra ovalis. The tympanum receives sound waves from the air; the attached stapes, acting freely in the hollow chamber, serves to transfer the sound signals from the tympanum to the inner ear through the fenestra ovalis, and the fenestra rotundum permits compensatory movements of the inner ear fluid between it and the fenestra ovalis when the apparatus functions.

In contrast, the middle ear apparatus of Sphenodon is much simpler in structure than that of the typical lizards (Fig. 53) and it functions in a different way (Wever, 1978). Despite the presence of a stapes and a fenestra ovalis on the lateral side of the braincase, Sphenodon has no conch-like basin on the quadrate and no pronounced retroarticular process to form the tympanic frame, no tympanum, no air-filled chamber for the free vibrations of the stapes, and no fenestra rotundum for compensatory movements of the inner ear fluid. A

Fig. 52. Typical middle ear apparatus of lizards. A, General relations of the middle ear and the inner ear structures in *Sceloporus magister* (from Wever, 1978). B, Temporal region of the skull of *Ctenosaura pectinata* in lateral view (After Oelrich, 1956). C, Braincase of an agamid lizard in lateral view, anterior to the right. Scale bars 5.0 mm.

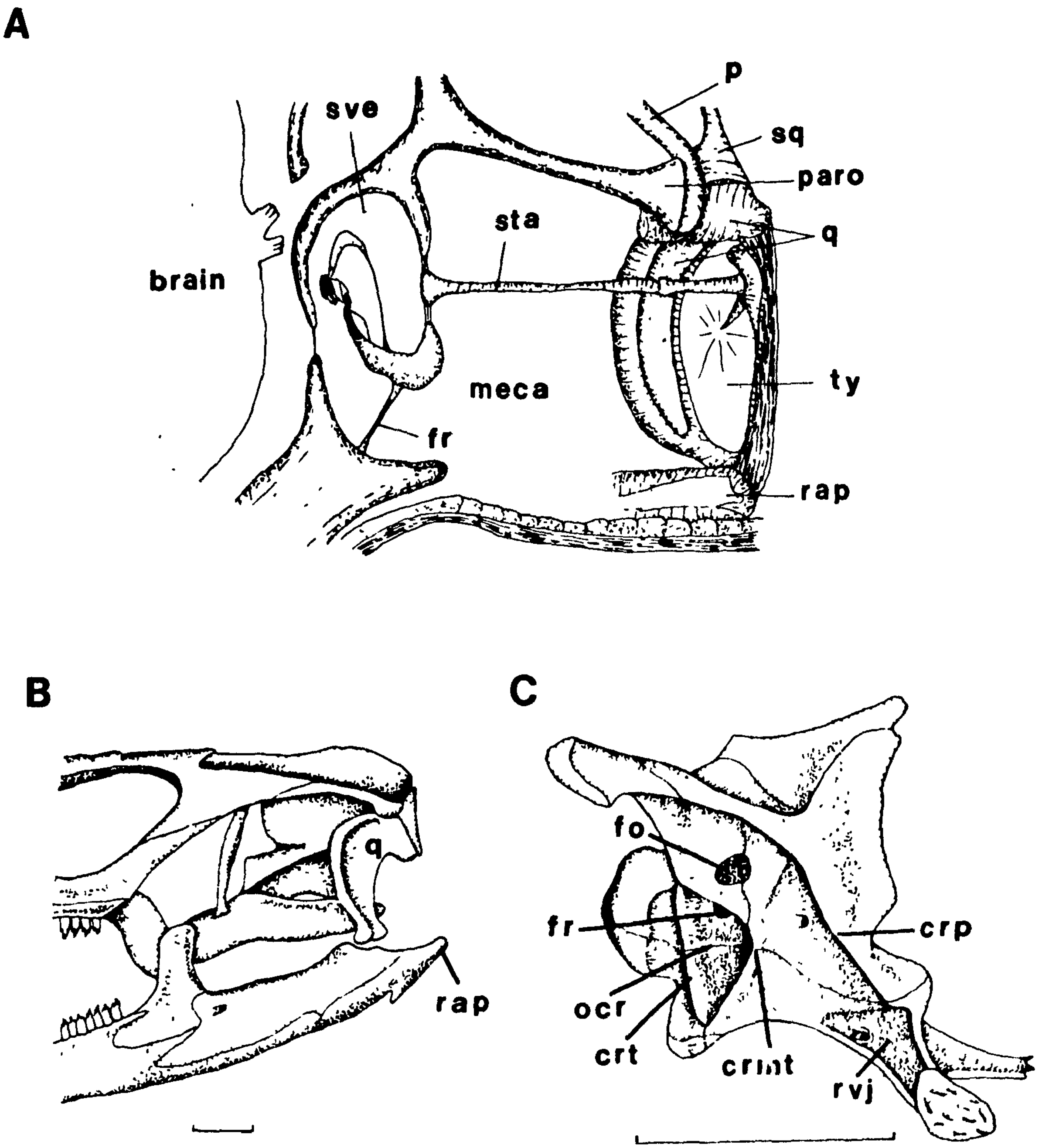

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Fig. 53. Middle ear apparatus of Sphenodon. A, General relations of the middle ear and the inner ear structures (from Wever, 1978). B, Temporal region of the skull in lateral view. C, Braincase in lateral view, anterior to the right. Scale bars 5.0 mm.

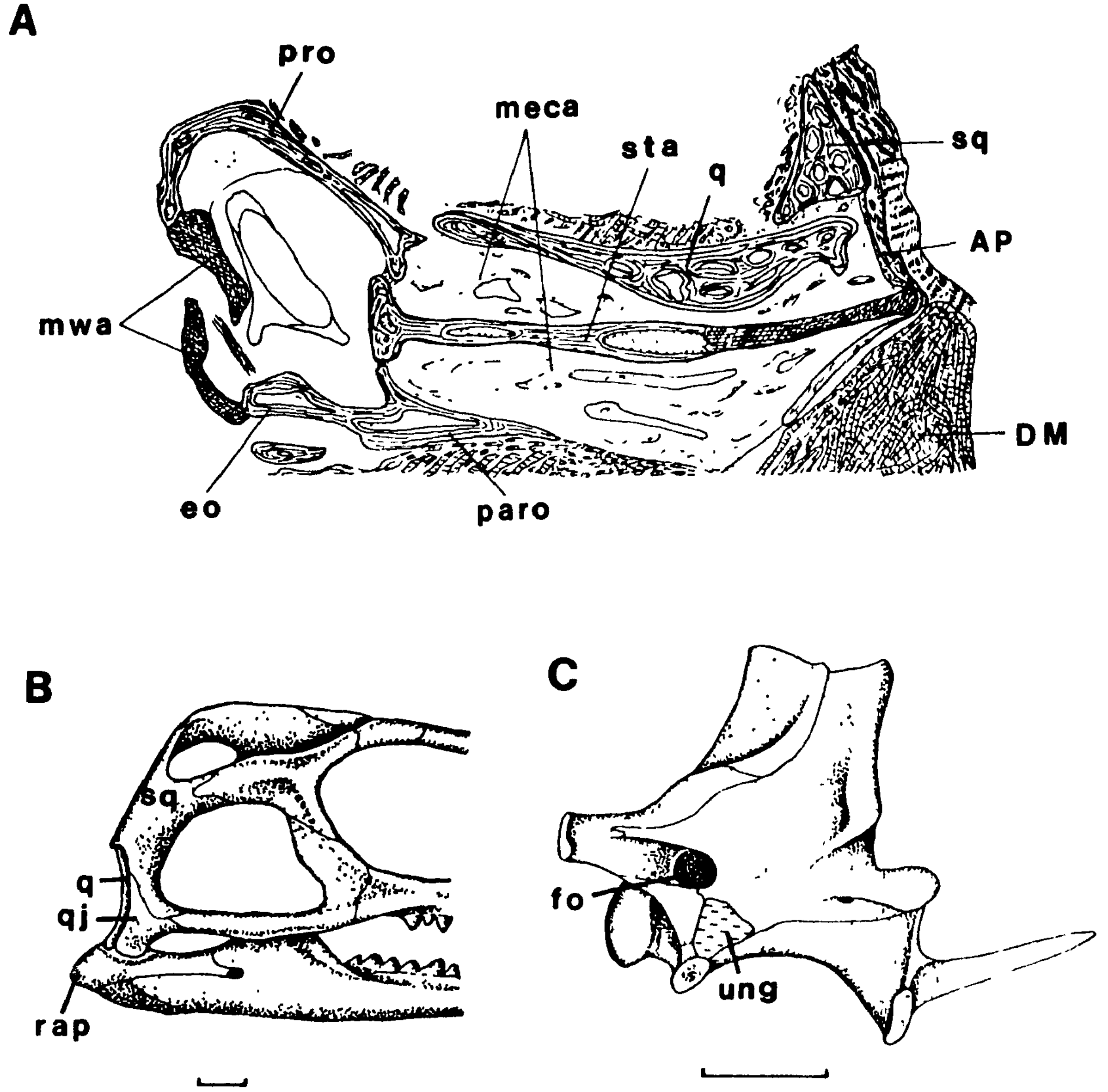
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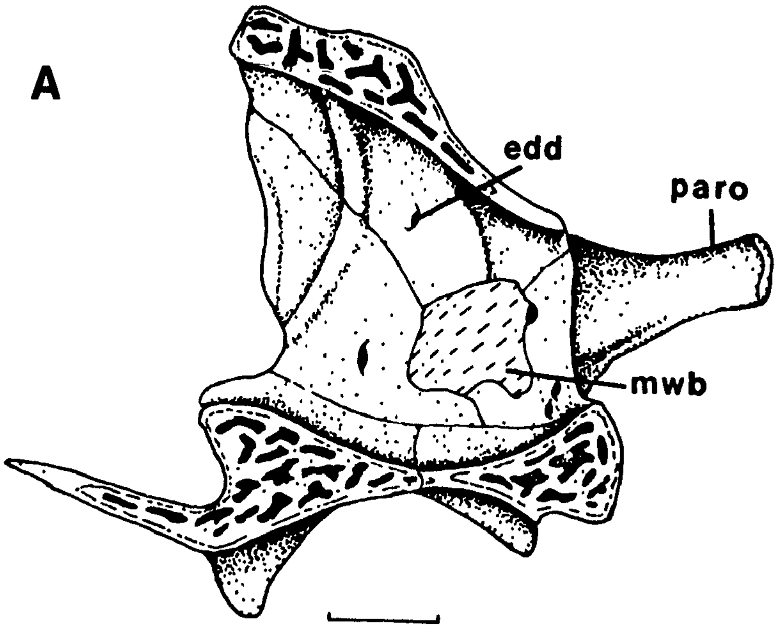
Fig. 54. Medial view of the braincases of A, <u>Sphenodon</u> and B, <u>Youngina</u> (after Evans, 1987). Scale bars 5.0 mm.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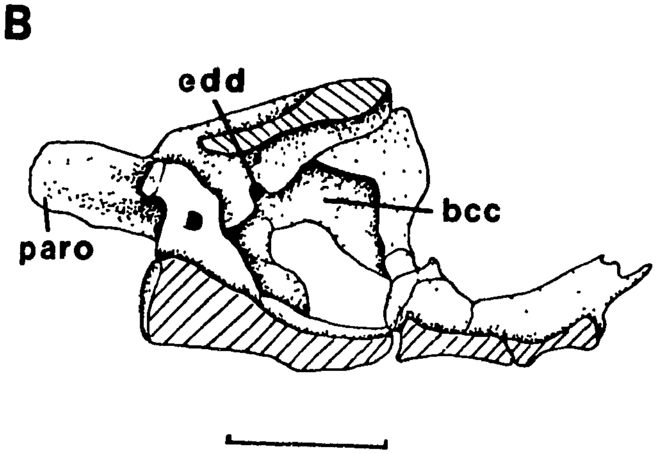
B
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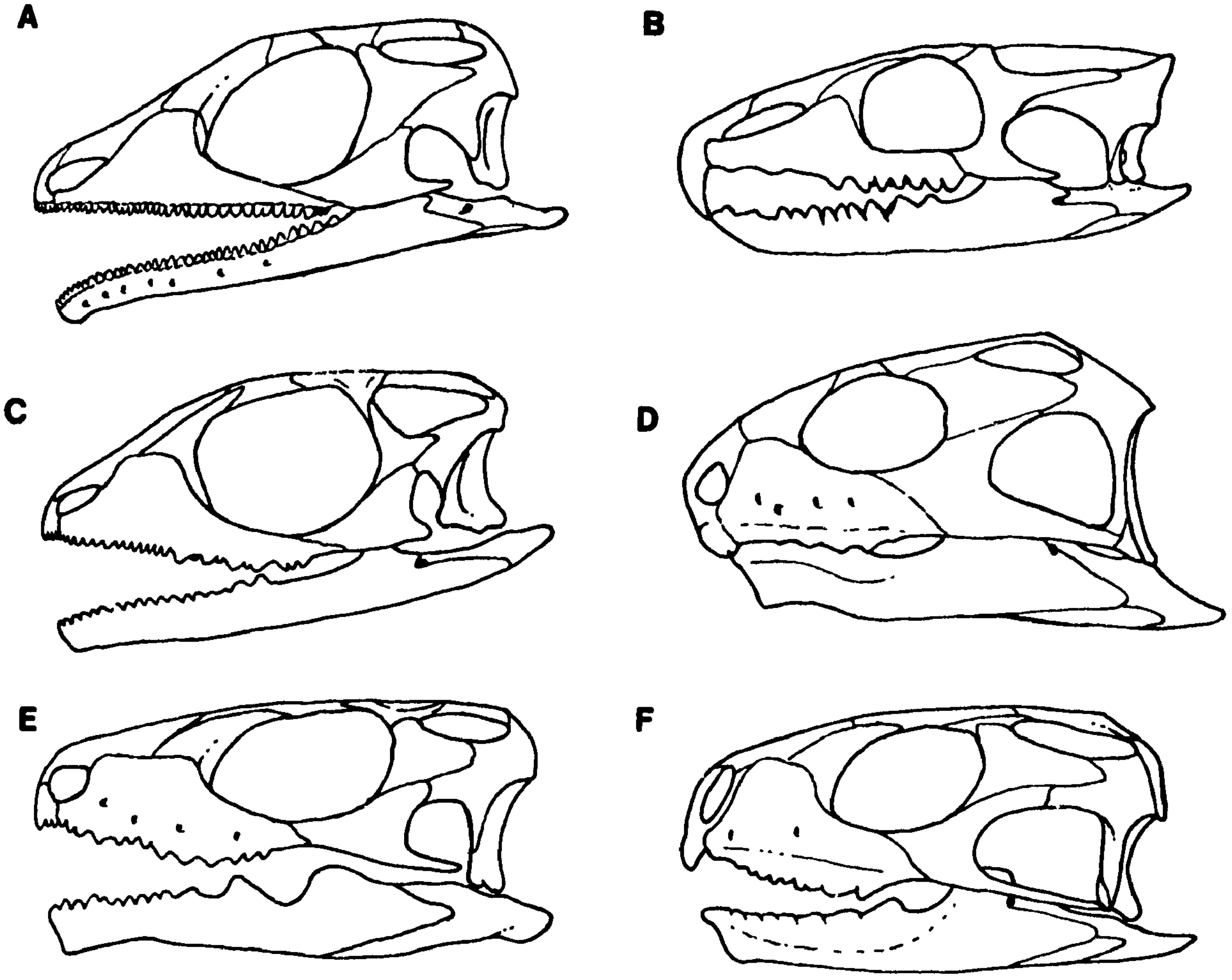
further difference is the presence of a gap in the lagena area of the medial wall of the otic capsule. As in the Permian lepidosauromorph _Youngina_, this area is not fully ossified (Fig. 54). Such a middle ear structure has traditionally been interpreted as a primitive pattern retained from the early diapsid condition.

Earlier work (Robinson, 1973; Evans, 1980; Fraser, 1982; Carroll, 1985; Whiteside, 1986) has shown that the fossil sphenodontidans from the Late Triassic-Early Jurassic had a tympanic frame made up of the quadratojugal (fused with the lateral side of the quadrate) and the squamosal (overlapping the lateral rim of the conch-shaped depression on the lateral surface of the quadratojugal-quadrate complex) as well as the quadrate and the retroarticular process (Fig. 55). In the retention of the quadratojugal and the contact of the squamosal, the middle ear apparatus of the early sphenodontidans differs from that of most lizards, but the tympanic frame could have functioned in comparable manner. The middle ear apparatus of lepidosaurs is closely associated with the quadrate region, the retroarticular process of the lower jaw and the braincase.

Asiacephalosaurus, the only known fossil sphenodontidan, has a well-preserved braincase showing a number of similarities with that of lizards. The most important structures of the braincase that are associated with the middle ear apparatus are the fenestra ovalis and the fenestra rotundum (the anterior subdivision of the fissura metotica).

Fig. 55. Lateral views of the skulls of A, Gephyrosaurus (after Evans, 1980), B, Palaeopleurosaurus (after Carroll, 1985), C, Diphydontosaurus (after Whiteside, 1986), D, Brachyrhinodon (after Fraser and Benton, 1989), E, Planocephalosaurus (after Fraser, 1982) and F, Clevosaurus (after Fraser, 1988).


A
B
C
D
E
F

The fenestra ovalis, which receives the footplate of the stapes, is present in every terrestrial vertebrate, while the fenestra rotundum is usually considered to be a uniquely derived structure of the Squamata. Sphenodon does not have the fenestra rotundum. However, the fenestra rotundum is clearly present in Asiacephalosaurus (Figs. 11, 14 and 56). This structure can also be recognized in Barojugalosaurus (Figs. 25 and 27). As in lizards, the fenestra rotundum of both genera is situated in the occipital recess (equivalent to the recessus scalae tympani + the occipital recess on the occipital bone; Oelrich, 1956). This strongly supports the conclusion that in the early history of the Sphenodontida some members had an impedance matching middle ear comparable to that of lizards in both morphology and function.

It is also significant that in the Late Triassic genus Diphydontosaurus, the basioccipital-exoccipital fragment shows an extensive lateral expansion posterior to the so-called fissura metotica (Fig. 57B). The least width of the lateral expansion reaches more than 50% of the total width of the occipital condyle as in Asiacephalosaurus and most lizards that possess a occipital recess. Such an extensive lateral expansion is also shown in the occipital of Gephyrosaurus (Fig. 57D). In contrast, Sphenodon (Fig. 57E) and the lizards in which the occipital recess and the fenestra rotundum have degenerated do not have such a lateral expansion. This lateral expansion forms the crista tuberalis and serves as the posterior wall of the occipital recess to separate the

Fig. 56. Reconstruction of the braincase of *Asiacephalosaurus wangi* in lateral view. Scale bar 5.0 mm.

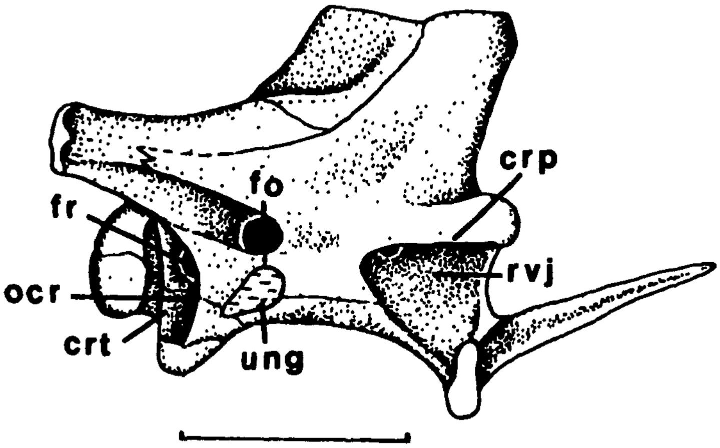

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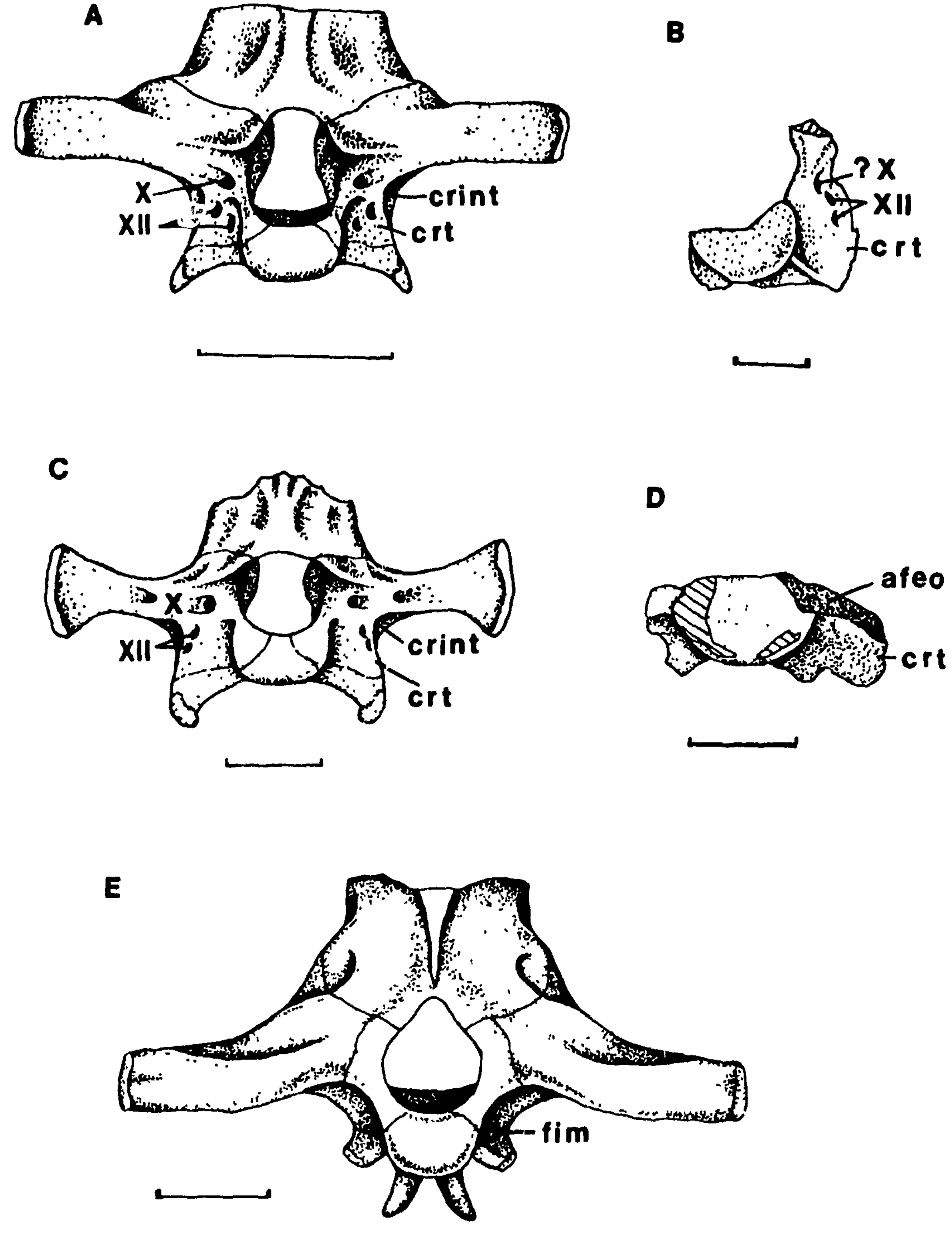
Fig. 57. Occipital views of the braincases or braincase fragments of A, Asiacephalosaurus, B, Diphydontosaurus (after Whiteside, 1986), C, Ctenosaura lizard (after Oelrich, 1956), D, Gephyrosaurus (after Evans, 1980) and Sphenodon. Scale bars 5.0 mm. in A, C, and E; 1.0 mm in B and D.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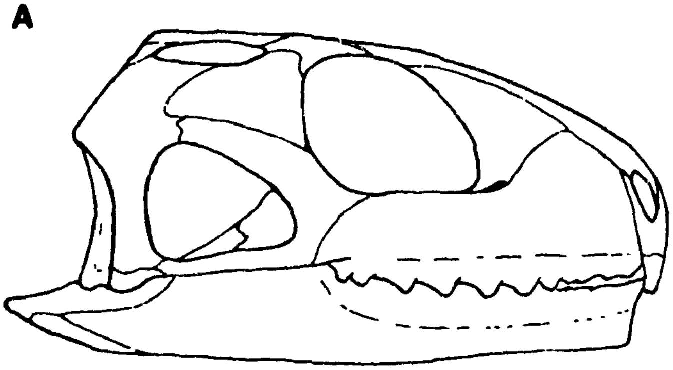
fenestra rotundum from the posteriorly positioned vagus foramen (the posterior subdivision of the fissura metotica) in Asiacephalosaurus and most lizards. To the best of my knowledge, all living lizards that have an occipital recess have a fenestra rotundum. On the other hand, the lateral closure of the occipital recess is correlated with the reduction of the crista tuberalis (i.e. the reduction of the lateral expansion of the basioccipital-exoccipital complex) in the majority of burrowing lizards and in the arboreal Chamaeleontidae (Rieppel, 1985). Therefore, the occurrence of the extensive lateral expansion of the basioccipital-exoccipital complex indicates that Diphydontosaurus and Gephyrosaurus may have possessed an occipital recess and a fenestra rotundum as in Asiacephalosaurus and most lizards. The dorsally positioned foramen in the exoccipital of Diphydontosaurus is probably the lateral exit for the vagus nerve. If this were the case, a lizard-style middle ear apparatus was characteristic of most known sphenodontidans of the early Mesozoic and arguably was the primitive condition. However, in a composite reconstruction of the braincase of Clevosaurus (Fraser, 1988), no occipital recess and no fenestra rotundum were restored.

Although a great many specimens of Late Jurassic-Early Cretaceous sphenodontidans have been collected, the anatomy of the middle ear region of these forms is not well documented. Based on specimen C.M. 6438 described in the previous section, a tympanic frame is probably present in Homoeosaurus *maximiliani*, but very distinct from that of either earlier genera or living *Sphenodon* (Fig. 58). The retroarticular process of the lower jaw does not seem as pronounced as in the earlier genera, but it is presumably not longer than that of *Sphenodon*. It is possible that the conch-like basin on the lateral side of the quadratojugal-quadrate complex is also not as well-developed as that of the Late Triassic-Early Jurassic forms. However, the remarkably elongated posterior process of the squamosal forms a notch-like structure on the posterolateral side of the skull. Such a notch presumably served as a tympanic frame for the tympanum as in an early crocodylomorph, *Dibothrosuchus* (Wu, 1986). If this were true, the tympanic frame of *Homoeosaurus maximiliani* shows a reverse configuration to that of the earlier sphenodontidans and most lizards (i.e. the longer support is at the top, rather than the bottom). All lizards without an occipital recess or fenestra rotundum lack a tympanum (such as *Anniella*, species in the Acontinae, etc; Rieppel, 1985). No known lizards possessing a tympanum lack the occipital recess and fenestra rotundum. If *Homoeosaurus maximiliani* had a tympanum, it could be inferred that, by analogy with lizards, it also had an occipital recess and the fenestra rotundum and therefore a functional middle ear, structurally similar to that of the early members except for the altered nature of the tympanic frame.

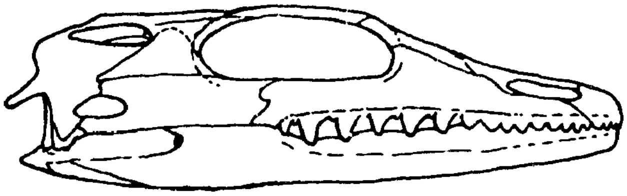
The shift of tympanic frame from ventral to dorsal support in *Homoeosaurus maximiliani* may have been related to

Fig. 58. Lateral views of the skulls of A, Asiacephalosaurus, B, Homoeosaurus maximiliani and C, Sphenodon.

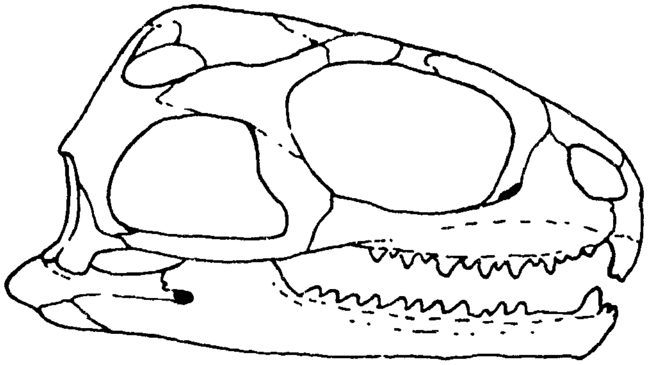
A



B



C



the development of a novel feeding mechanism. Whiteside (1986) states that the reduction of the tympanic frame and the loss of the tympanum in Sphenodon is probably correlated with the development of a tongue feeding mechanism, as in chamaeleontid lizards. This feeding method needs a quick jaw-opening action to enable the tongue to eject in as short a time as possible. If we consider the lower-jaw as a lever system, with the fulcrum at the quadrate articulation, the retroarticular process functions as an effort lever arm, with the M. depressor mandibulae inserting on its posterior end and exerting force to open the jaws (the output lever). Mechanically, a relatively short effort arm will produce a faster action in a lever system. This may explain the reduced length of the retroarticular process in Sphenodon and Homoeosaurus maximiliani. With the shortening of the retroarticular process the M. depressor mandibulae would move towards the quadrate articulation and so reduce the space for a tympanum, as seen in chamaeleontid lizards. This assumes that selective pressures for change in the jaw apparatus were greater than those for maintaining the impedance matching middle ear.

In contrast, tongue feeding mechanism could have evolved in Homoeosaurus maximiliani while a space for the attachment of a tympanum retained through the elongation of the posterior process of the squamosal. With the elongation of the process the origin of the M. depressor mandibulae may have moved posterodorsally to leave a space dorsally for support of the tympanum. In this way, the tympanic frame shifted from ventral to dorsal support in this species.

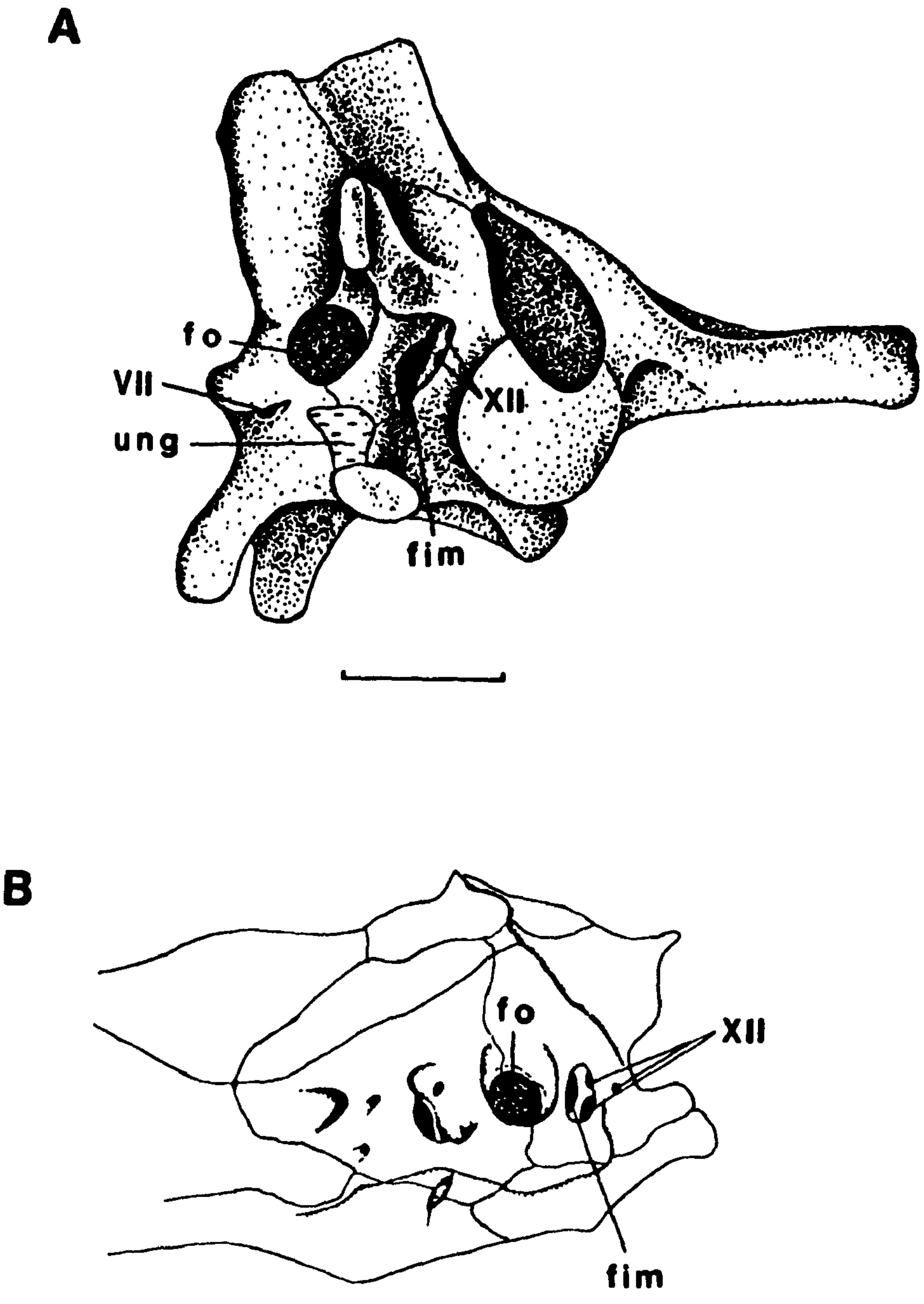
The loss of a tympanum is not associated solely with the development of tongue feeding. The reduction of the tympanum in the ancestors of Sphenodon may have been related to its burrowing life habit as in the majority of burrowing lizards. The peculiarly elongated limbs indicate that Homoeosaurus maximiliani was not a burrower, but more probably an active terrestrial animal. In this habitat, there would have been strong selective pressure to a well-functioning impedance matching middle ear in addition to jaw mechanics suitable for tongue feeding. The unique structure of the tympanic frame may represent a resolution of these two apparently conflicting biomechanical requirements.

This study shows that the fossil members of the Sphenodontida probably possessed an impedance matching middle ear. This discovery supports the hypothesis that the so-called "primitive" aspects of the middle ear device of the living Sphenodon are actually derived and have evolved within the group.

The reduction of the tympanic frame and the loss of the tympanum in Sphenodon are probably related to both the development of a tongue feeding mechanism and the adaptation to a burrowing life habit. Although Sphenodon does not have an air-filled middle ear cavity or tympanum, but possesses a space containing the usual blood vessels and nerves seen in the middle ear cavity of typical lizards, and a layer of dense connective tissue known as the aponeurosis and considered by Huxley (see Gans and Wever, 1976) and others as a remnant of the tympanic membrane. Together with the skin and the M. depressor mandibulae, it forms a sound-receptive surface. Sphenodon has a slender stapes almost identical with those of Asiacephalosaurus and most lizards that can only be considered as a remnant of a structure that once functioned in an impedance matching middle ear (Carroll, 1988a). Sphenodon has neither an occipital recess nor a fenestra rotundum, nor is the fissura metotica divided. Similarly, extant lizards without a tympanum have closed the occipital recess and reduced the fenestra rotundum, although the fissura metotica retains a medial subdivision (Rieppel, 1985). As with Sphenodon, most of these lizards have adapted to a burrowing life habit. An undivided fissura metotica was an universal phenomenon in primitive reptiles and occurs in the early stage of the embryo of squamates (de Beer, 1985 edition) and the adults of Sphenodon and Acrochordus snakes (Rieppel, 1980). This is undoubtedly a primitive character in reptiles. However, Rieppel (1979 and 1985) argued that Acrochordus snakes are the sister-group of the most advanced snakes--the colubroids--and considered that the undivided fissura metotica was a derived feature resulting from paedomorphism. A similar explanation can be applied to Sphenodon.

The lateral exits for cranial nerve XII open on the posterior wall of the undivided fissura metotica in both Sphenodon and Acrochordus snakes (Fig. 59). In this aspect,

Fig. 59. Braincases of A, Sphenodon in posterolateral view and B, The snake Acrochordus snake in lateral view (after Rieppel, 1980). Anterior is to the left. Scale bars 5.0 mm.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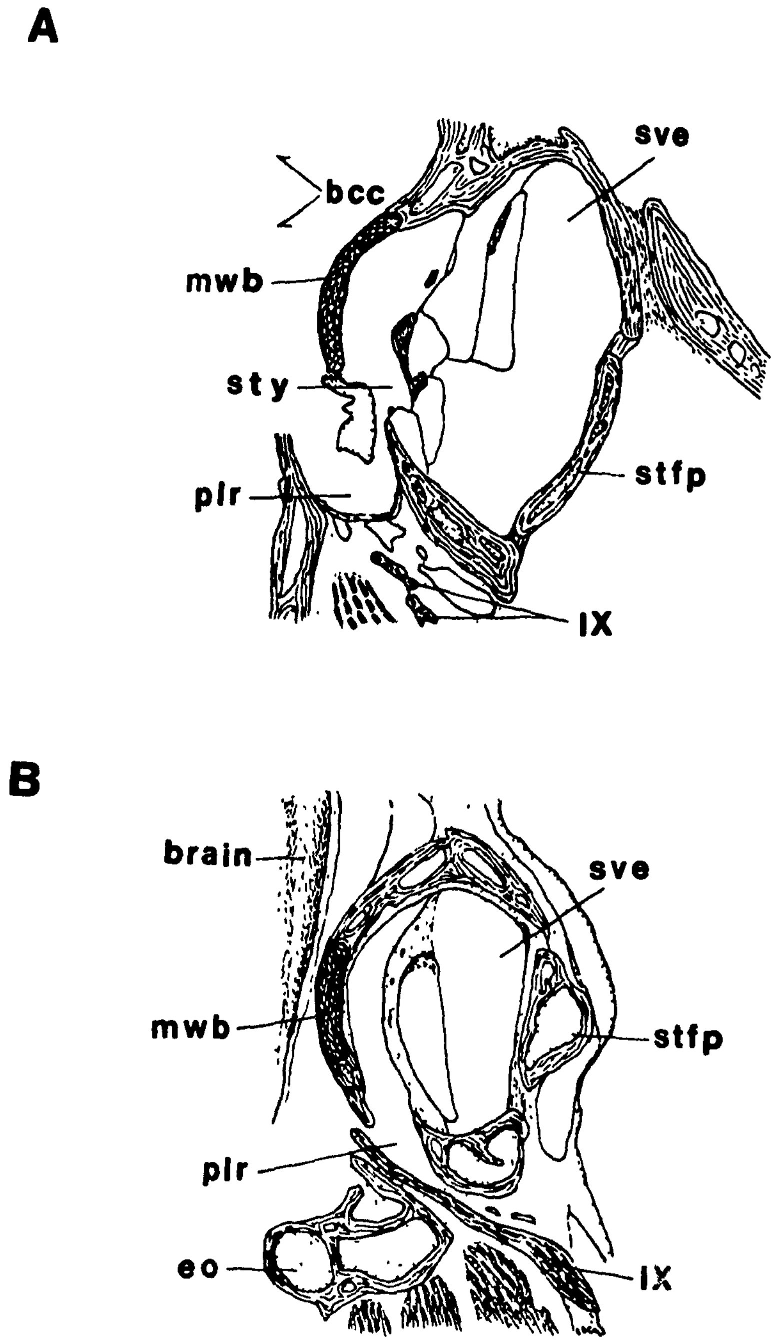
these animals differ as adults from primitive reptiles and the early stages of the squamate embryo in which the undivided fissura metotica is widely separated from the exits for cranial nerve XII. The primitive condition is also expressed in early embryonic stages of *Sphenodon* and *Acrochordus* snakes. It is obvious that merging of the exits for cranial nerve XII into the fissura metotica is a derived feature in the Lepidosauria; this feature must have been independently developed in *Sphenodon* and *Acrochordus*. We do not know what the function of the confluence of the fissura metotica and the lateral exits of cranial nerve XII may be, but it might be related to the altered compensatory circuit for the inner ear fluid. As for the incompletely ossified medial wall of the otic capsule of *Sphenodon*, there is an evident parallel in lizards with a reduced middle ear apparatus. Wever (1978) notes that the otic capsule of *Chamaeleo chamaeleon calcarifer* is not entirely ossified medially; rather it is separated from the brain by a thin membrane as in *Sphenodon* (Fig. 60).

This study has shown that there are three patterns of the middle ear apparatus in the order Sphenodontida. These patterns appear to display a successive sequence on the basis of their occurrence in geological time, i.e. from a lizard-style middle ear in the Late Triassic-Early Jurassic members through a modified one with a reversed tympanic frame in the Late Jurassic *Homoeosaurus maximiliani* to the reduced pattern of the living genus *Sphenodon*. However, exact relationships

Fig. 60. Frontal sections through the otic capsules of A, *Sphenodon* (after Wever, 1978) and B, *Chamaeleo chamaeleon calcarifer* lizard (after Wever, 1978); showing the membranous medial wall of the otic capsule.


A
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sty
stfp
plr
IX
B
brain
sve
mwb
stfp
plr
eo
IX

among the three patterns can not be specified at present since we do not have any information on the middle ear apparatus of the other Late Jurassic-Early Cretaceous sphenodontidans, nor from any fossils since the Early Cretaceous.

FUNCTIONAL ANALYSIS OF THE TEMPORAL REGION

Although the the basic pattern of the middle ear apparatus is very similar in the early members of the Sphenodontida and squamates, the squamates alone possess a streptostylic quadrate, a feature that is very consistent in the history of the group. In the most primitive sphenodontidans so far known, Gephyrosaurus and Diphydontosaurus, (Whiteside, 1986; Evans, 1988; Gauthier et al., 1988; Fraser and Benton, 1989), the lower temporal bar is incomplete, but the quadrate is fixed to the skull. Based on many synapomorphies, the Sphenodontida and the Squamata share a more recent common ancestor with one another than either does with any other group of lepidosauromorphs (Benton, 1985; Carroll, 1985, 1988a and 1988b; Evans, 1988; Gauthier et al, 1988). If the lizard-like impedance matching middle ear is considered a synapomorphy of the Lepidosauria, was the fixed quadrate of the Sphenodontida or the streptostylic quadrate of the Squamata retained from their common ancestor? It is difficult to clarify this question based on knowledge currently available from the fossil record.

The study of the adductor jaw musculature and associated bony structures is extremely important in elucidating the pattern of evolution and the origin both of the feeding mechanism and hearing apparatus of various vertebrate groups (Schaeffer and Rosen, 1961; Romer, 1956; Barghusen, 1972; Crompton and Parker, 1978; Bramble, 1978; Carroll and Holmes, 1980). In both Sphenodontida and Squamata, the middle ear and the jaw apparatus form an integrated complex associated with the quadrate, hence it is probable that study of this system would shed some light on the question of the primitive nature of the quadrate.

Cranial Muscles Innervated by the Trigeminal Nerve

Cranial muscles of Sphenodon and lizards, particularly those innervated by the trigeminal nerve, have been described by many authors: Sphenodontida by Poglayen-Neuwall (1953), Ostrom (1962), Haas (1973), and Gorniak et al. (1982) and Squamata by Oelrich (1956), Haas (1973), Throckmorton (1976, 1978 and 1980), Rieppel (1978), and Smith (1980 and 1982). The trigeminal nerve innervates three major cranial muscles: the adductor mandibulae, the constrictor internus dorsalis, and the constrictor ventralis trigemini. The first two will be examined and compared between Sphenodon and lizards. The terminology of the adductor mandibulae and constrictor internus dorsalis was established by Luther (1914) and Lakjer (1926) and has been used by most recent authors. The name of each muscle used in the present study is derived from Haas (1973).

As previous descriptions noted, individual variation of these muscle groups seems to be very common in Sphenodon. Therefore, additional dissection was undertaken in order to corroborate details and provide a tangible basis for comparison with squamates and fossil forms. For squamates, the head musculature of Ctenosaura pectinata (Oelrich, 1956) was chosen as a standard pattern for comparison. An individual of Japalura laviceps (an agamid lizard from China) was also dissected. The following description of the cranial muscles of Sphenodon will be based on my dissection unless specialized otherwise.

a. Adductor mandibulae

The M adductor mandibulae has three units: The M. adductor mandibulae externus, lying lateral to the maxillary (V2) and anterior to the mandibular (V3) branches of the trigeminal nerve, the M. adductor mandibulae internus located medial to the maxillary and anterior to the mandibular branches, and the M. adductor mandibulae posterior, positioned lateral to the maxillary and posterior to the mandibular branches. Each of these three parts can be further subdivided (Table 2).

M. adductor mandibulae externus superficialis

In Sphenodon, the M. adductor mandibulae externus superficialis consists of three portions: the M. retractor anguli oris, the M. levator anguli oris and the M. adductor mandibulae externus superficialis sensu stricto. However, the M. retractor anguli oris has not been distinguished in squamates.

Table 2. Cranial muscles innervated by the trigeminal nerve

M. adductor mandibulae

- M. adductor mandibulae externus
    - M. adductor mandibulae externus superficialis
        - M. levator anguli oris
        - M. retractor anguli oris
        - MAME. Superficialis *sensu stricto*
    - M. adductor mandibulae externus medialis
    - M. adductor mandibulae externus profundus
- M. adductor mandibulae internus
    - M. pseudotemporalis
        - M. pseudotemporalis superficialis
        - M. pseudotemporalis profundus
    - M. pterygoideus
        - M. pterygoideus typicus
        - M. pterygoideus atypicus
- M. adductor mandibulae posterior

M. Constrictor internus dorsalis

- M. levator pterygoidei
- M. protractor pterygoidei
- M. levator bulbi

The M. retractor anguli oris is very thin and triangular in Sphenodon (Figs. 61 and 62A). It arises mainly by a sheet-shaped tendon, but its posteriormost fibers originate directly from the medial surface of the ventral half of the descending process of the squamosal. A few short posteroventral fibers originate from the suture of the squamosal to the quadratojugal at the posteroventral corner of the lower temporal fenestra, but none from the lower temporal bar itself. The muscle fibers run anteroventrally and insert along the dorsalmost margin of the lateral rictal plate.

The M. levator anguli oris is a small, strap-shaped muscle (Figs. 62A and 63A) originating by a weak tendon from a limited region on the medial surface near the suture of the postorbital with the postfrontal. The muscle is slightly deeper in position than the M. adductor mandibulae externus superficialis sensu stricto. Its fibers extend medial to the postorbital bar almost vertically but slightly posteriorly and insert on the dorsal margin of the anteromedial surface of the medial rictal plate. There is no additional origin of the muscle.

In Ctenosaura, the M. levator anguli oris is much larger than that in Sphenodon and covers most of the lower temporal fenestra (Fig. 62B). It originates more dorsally than in Sphenodon, from the dorsal half of the tympanic crest of the quadrate and from the squamosal and postorbital along the ventrolateral margin of the upper temporal bar. The muscle fibers are more vertically oriented than in Sphenodon and

Fig. 61. Lateral and slightly ventral view of the superficial muscles of the head of *Sphenodon punctatus*.

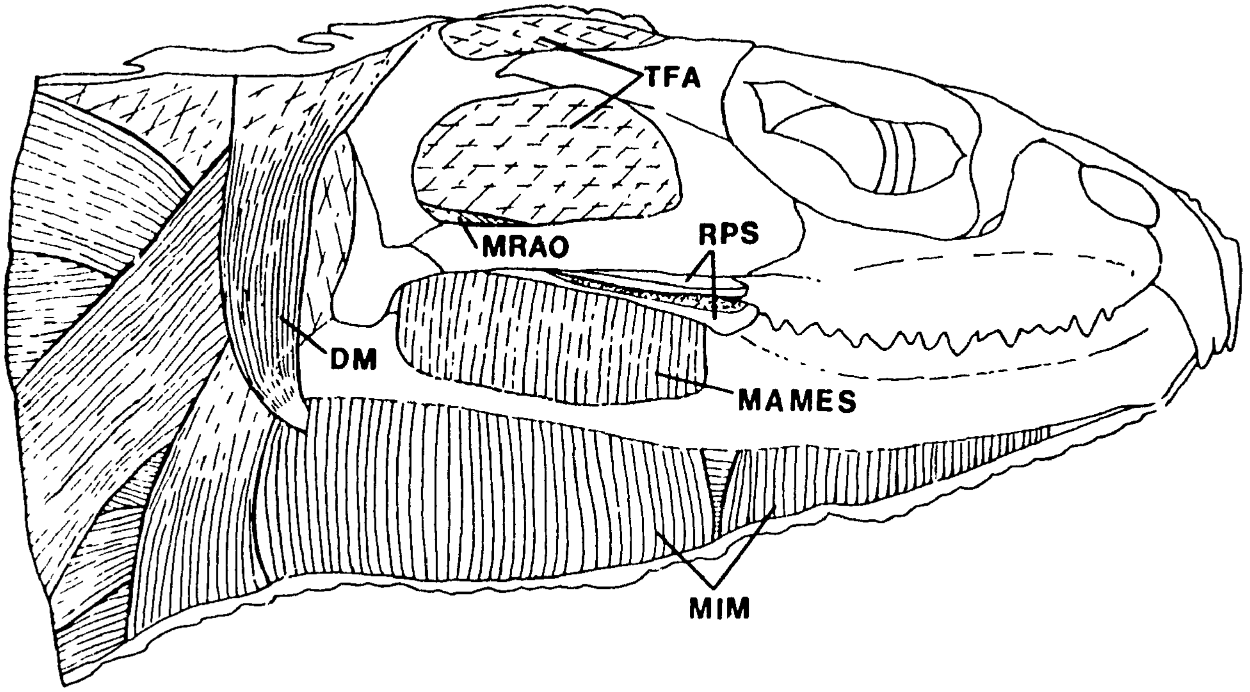
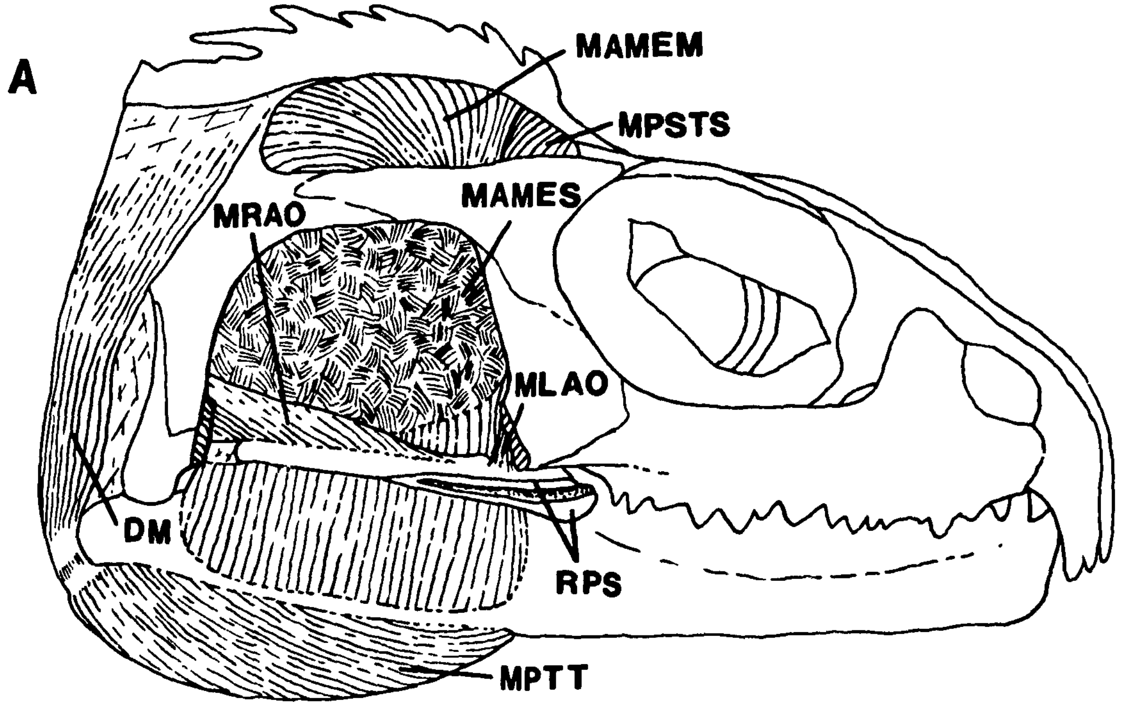

TFA
MRAO
RPS
DM
MAMES
MIM

Fig. 62. Lateral views of the cranial muscles of A, *Sphenodon punctatus* and B, *Ctenosaura pectinata* (after Oelrich, 1956).


A
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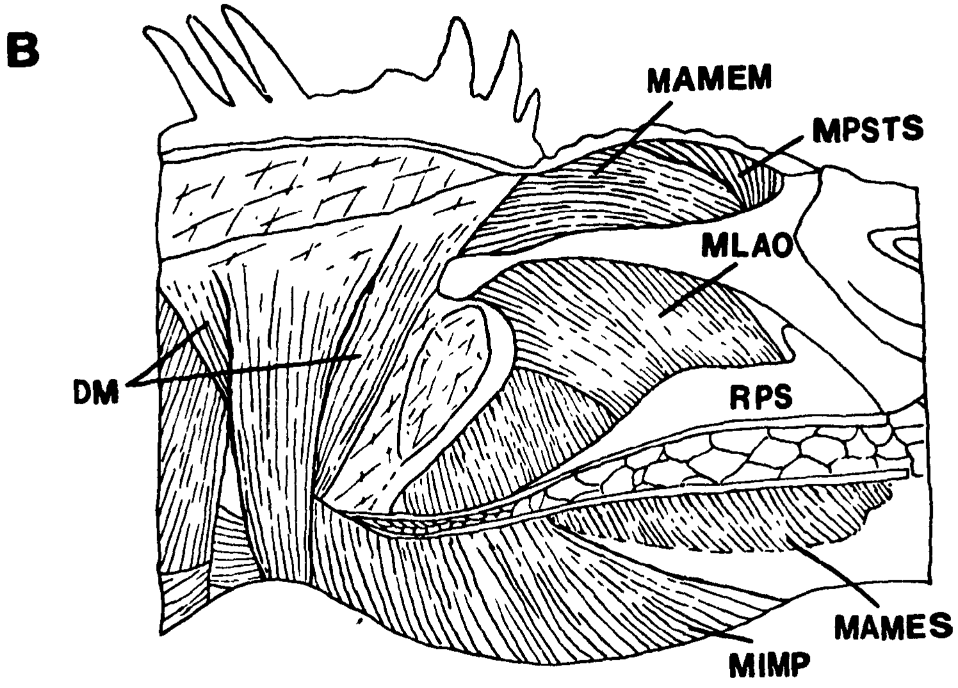
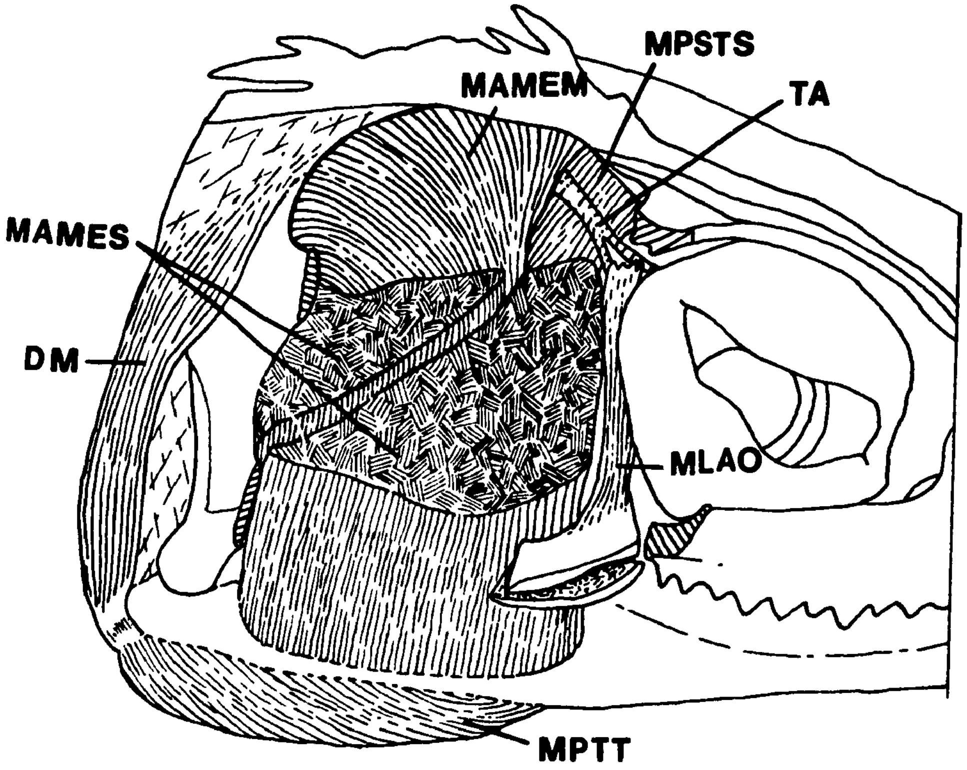
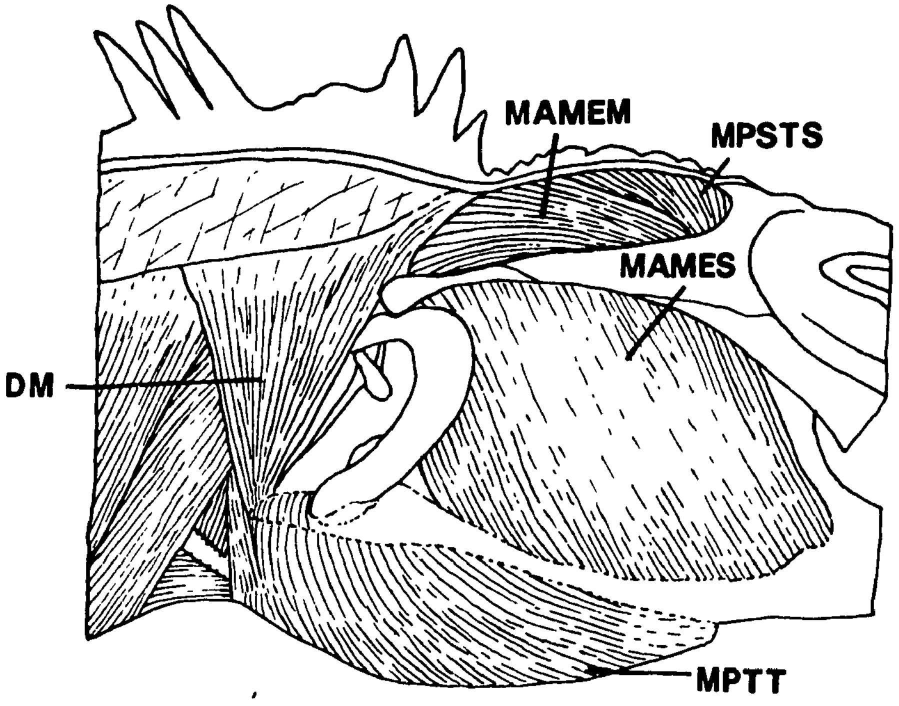

B
MAMEM
MPSTS
MLAO
DM
RPS
MAMES
MIMP

Fig.63. Lateral views of the cranial muscles of A, Sphenodon punctatus and B, Ctenosaura pectinata (after Oelrich, 1956).

A



B



insert on the dorsomedial surface of rictal plates.

The M. adductor mandibulae externus superficialis *sensu stricto* in *Sphenodon* bulges into the inferior temporal fenestra and has a expansive origin from the inferior temporal facia (Fig. 61), the entire medial surface of the upper temporal bar, the posteromedial surface of the dorsal process of the jugal and the medial surface of the descending process of the squamosal along the anterior and posterior margins of the inferior temporal fenestra. The muscle can be separated into a large anterolateral and a small posteromedial portion (Fig. 63A). In common with the M. retractor anguli oris, its fibers run almost vertically and slightly posteriorly, to insert on the lateral surface of the mandible posterior to the marginal tooth row of the dentary. More medial fibers insert on the dorsolateral margin of the postcoronoid region and on the lateral surface of the basal aponeurosis.

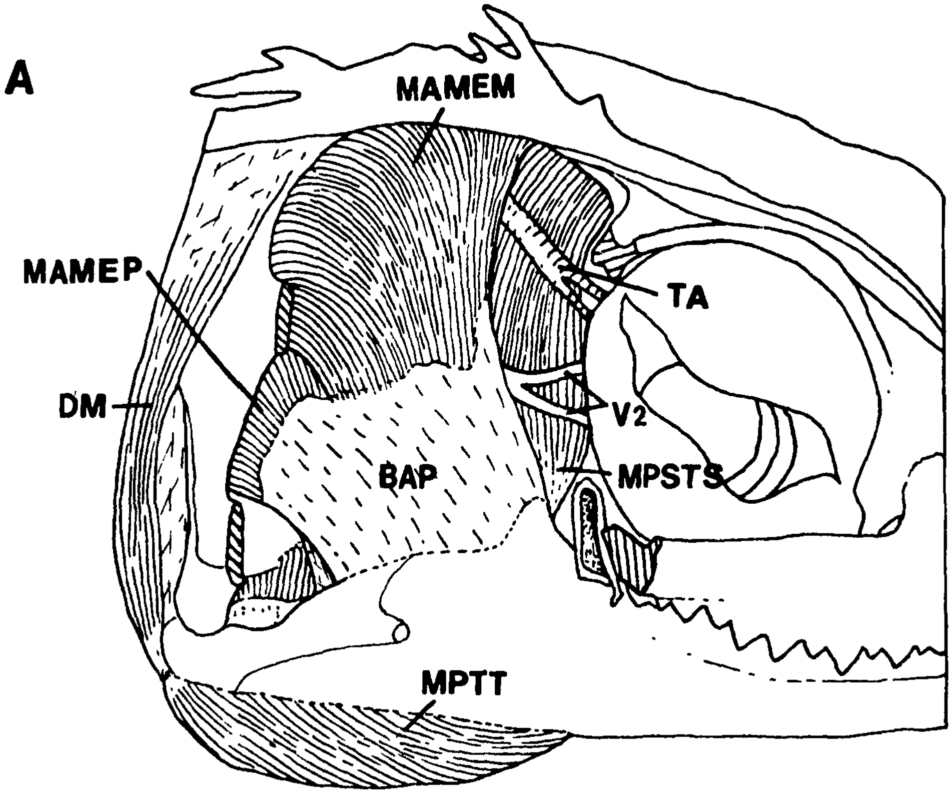
In *Ctenosaura*, the muscle has similar origins and insertions. Since the inferior temporal facia is not developed, most of its fibers arise directly from the bones around the inferior temporal fenestra (Fig. 63B). A tendinous sheet from the ventromedial surface of the squamosal serves for the origin of some fibers. The muscle fibers extend anteroventrally, showing an orientation opposite to those of *Sphenodon*.

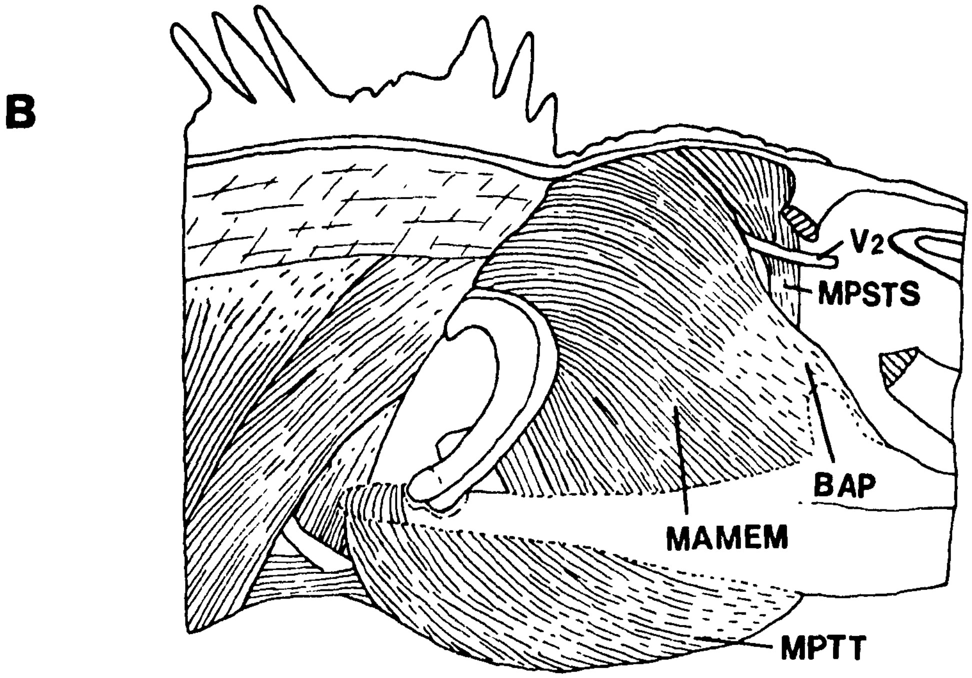
M. adductor mandibulae externus medialis

The M. adductor mandibulae externus medialis fills most of the supratemporal fenestra in Sphenodon (Figs. 62A and 63A). It arises from the posterior two thirds of the medial shelf of the supratemporal fenestra including the parietal and squamosal and from the medial surface of the squamosal at the posterolateral corner of the fenestra (Fig. 64A). Its fibers extend first anteriorly and then anteroventrally, and insert on the anteromedial surface of the basal aponeurosis that attaches to the dorsalmost margin of the lateral surface of the coronoid process and the postcoronoid region. The posterolateral fibers of the muscle insert on the dorsolateral border of the aponeurosis. The M. adductor mandibulae externus medialis can be readily separated from adjacent muscles based on fiber direction, but it shows poor intramuscular subdivisions. As Polayen-Neuwall (1953) described, the fibers that come from the upper temporal bar have a more vertical orientation and belong to the M. adductor mandibulae externus superficialis sensu stricto rather than to this muscle.

In Ctenosaura, the M. adductor mandibulae externus medialis has a more extensive origin than in Sphenodon. It arises from the posterior wall of the inferior temporal fenestra formed by the quadrate (Fig. 64B) as well as from the posterior and medial walls (shelf) of the supratemporal fenestra. The fibres extend anteroventrally, but more obliquely than in Sphenodon. The fibers from the supratemporal walls converge anteroventrally and insert on the basal aponeurosis (the bodenaponeurosis, Oelrich, 1956), while the fibers from the inferior temporal wall insert not only on the

Fig. 64. Lateral views of the cranial muscles after removal of the superficial muscles. A, *Sphenodon punctatus* and B, *Ctenosaura pectinata* (after Oelrich, 1956).


A
MAMEM
MAMEP
TA
DM
V2
BAP
MPSTS
MPTT


B
V2
MPSTS
BAP
MAMEM
MPTT

posterior border of the basal aponeurosis but also directly on the dorsomedial edge of the postcoronoid area of the mandible.

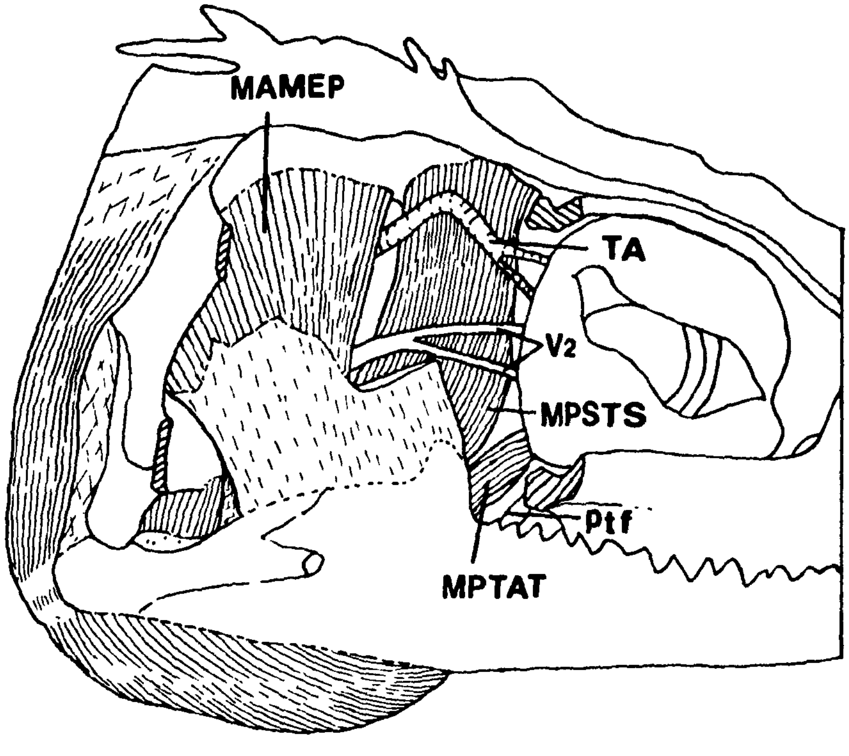
M. adductor mandibulae externus profundus

The M. adductor mandibulae externus profundus in <u>Sphenodon</u> (Fig. 65A) shows a configuration very similar to that illustrated by Poglayen-Neuwall (1953). The muscle originates primarily from the posterior wall of the supratemporal fenestra and its posteroventral fibers arise from the posterodorsal process of the prootic (Haas, 1973). The current dissection shows that the posteroventral fibers arise mainly from the lateral aspect of the anteromedial process of the squamosal and the dorsolateral surface of the pterygoid ramus of the quadrate posterior to the insertion of the M. adductor mandibulae posterior (Fig. 66A). The muscle fibers converge anteroventally and insert on the posteromedial surface of the basal aponeurosis.

In <u>Ctenosaura</u>, the M. adductor mandibulae externus profundus differs from that in <u>Sphenodon</u> in that it fans anteroventrally rather than posterodorsally. Its fibers originate from the ventrolateral and ventromedial surfaces of the posterolateral wall of the supratemporal fenestra formed by the parietal and supratemporal as well as from the dorsolateral surface of the posterior process of the prootic. The fibers insert mainly on the medial surface of the basal aponeurosis (Fig. 66B).

Fig. 65. Lateral views of the medial adductor jaw muscles of A, *Sphenodon punctatus* and B, *Ctenosaura pectinata* (after Oelrich, 1956).

A



B

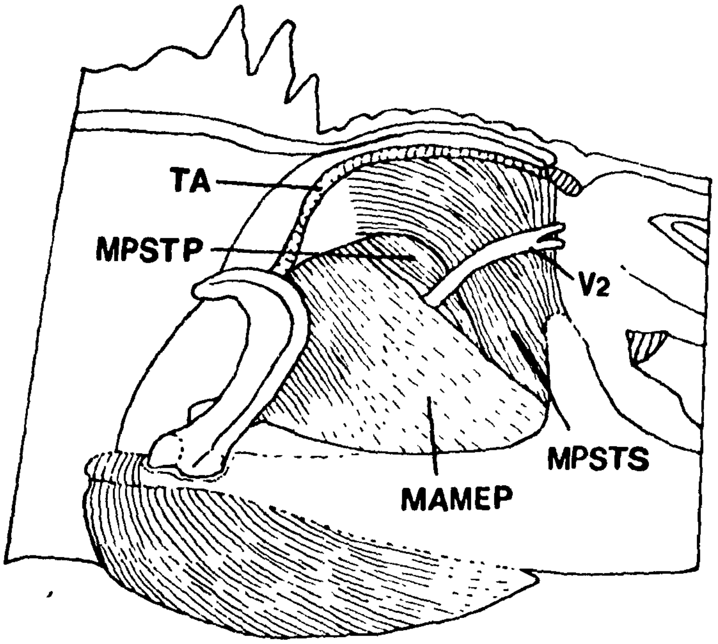
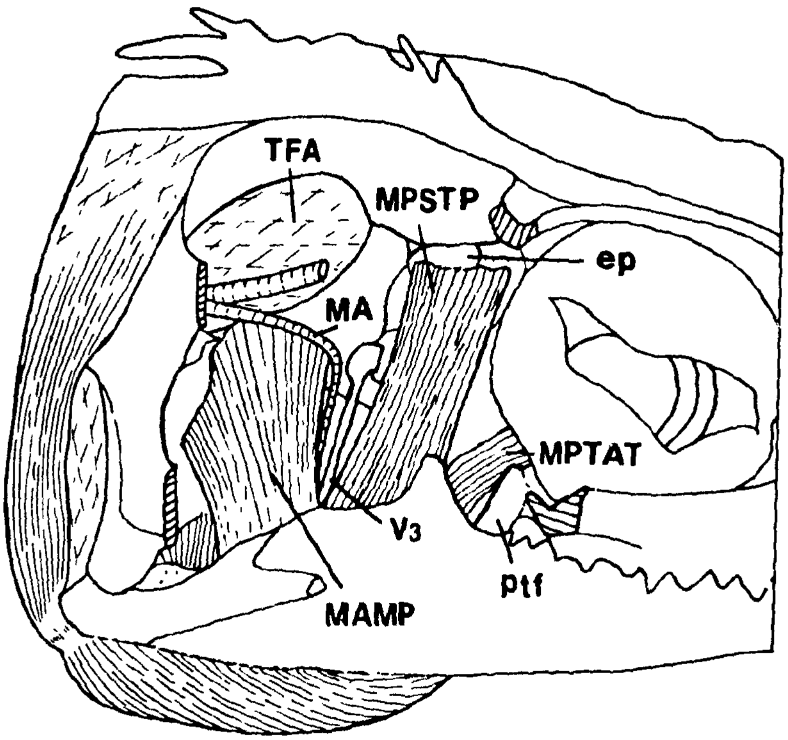
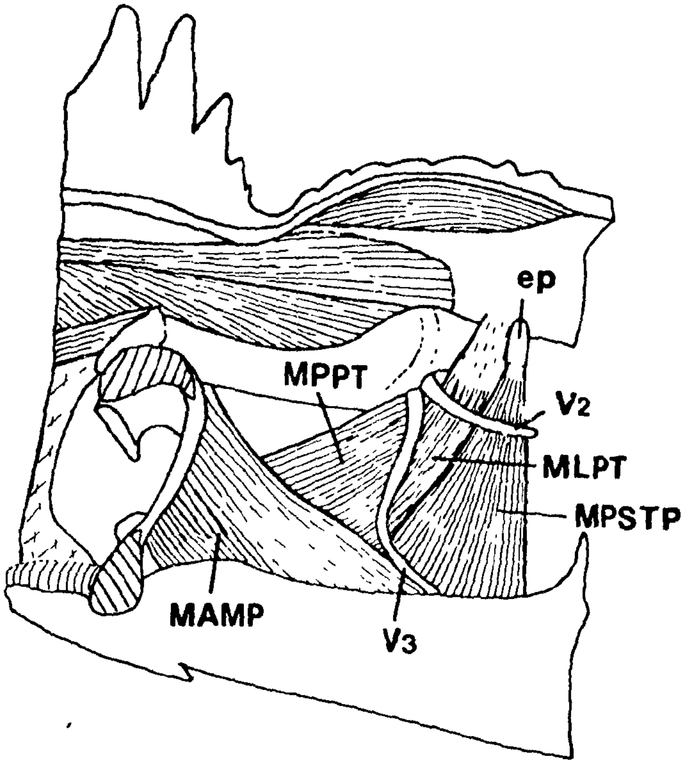


Fig. 66. Lateral views of the deep adductor jaw muscles of A, *Sphenodon punctatus* and B, *Ctenosaura pectinata* (after, Oelrich, 1956).

A



B



M. pseudotemporalis

Two distinct parts of the M. pseudotemporalis can be recognized in both Sphenodon and Ctenosaura: the M. pseudotemporalis superficialis and the M. pseudotemporalis profoundus.

The M. pseudotemporalis superficialis bulges through the anteromedial part of the supratemporal fenestra in Sphenodon. It originates from the anterior third of the medial shelf of the supratemporal fenestra, which is formed by the anterior part of the parietal and the posterior part of the postfrontal (Fig. 65A). Some medial fibers come from the dorsalmost part of the epipterygoid (Fig. 66A). An internal tendon reported in previous studies is very small. As with the M. adductor mandibulae externus superficialis sensu stricto, the fibers of the M. pseudotemporalis superficialis extend ventrally and slightly posteriorly, and attach to the anterior half of the ventromedial surface of the basal aponeurosis.

In Ctenosaura, the M. pseudotemporalis superficialis shows a more extensive origin than in Sphenodon. In addition to the bones described in Sphenodon, the fibers also arise from the lateral surface of the alar process of the prootic, dorsal to the trigeminal nerve (Fig. 66B). The fibers extend ventrally and anteriorly rather than ventrally and posteriorly as in Sphenodon and mainly insert on the medial surface of the basal aponeurosis. The anterior fibers attach directly to the posteromedial margin of the coronoid process.

The M. pseudotemporalis profundus is a thin, rectangular muscle positioned lateral and anterior to the epipterygoid in Sphenodon (Fig. 66A). Its fibers are more oblique than those of the superficial part, extending ventrally and posteriorly and inserting on the ventromedial surface of the coronoid and the anterior part of the medial surface of the surangular. The muscle originates from the dorsal part of the epipterygoid and the anterodorsal wall of the braincase. No fibers of the muscle arise from the descending process of the parietal (the medial shelf of the supratemporal fenestra) as was described in Haas' study (1973).

In Ctenosaura, the M. pseudotemporalis profundus is a small triangular muscle lying lateral and posterior to the epipterygoid (Fig. 66B). Its anterior fibers extend almost vertically, and the posterior fibers fan posteroventrally, displaying a similar direction to that of the muscle in Sphenodon. The muscle arises from the anterior, lateral, and posterior surfaces of the ventral two-thirds of the epipterygoid and inserts on the posteromedial surface of the coronoid and anteromedial surface of the surangular.

M. pterygoideus

The M. pterygoideus in Sphenodon consists of a large posterior mass, the M. pterygoideus typicus, and a very small anterior one, the M. pterygoideus atypicus. Lizards have only the M. pterygoideus typicus that was termed the M. pterygomandibularis (Oelrich, 1956).

The M. pterygoideus typicus is the largest single muscle in Sphenodon, bulging ventrally lateral to the pharynx (Fig. 67A). This pinnate muscle can be separated into a small lateral and a very large medial portion by the different origins of the fibers. The lateral portion arises by a tendon from the ventrolateral tip of the pterygoid flange. The fibers of the medial mass originate from the anteroventral surface of the pterygoid flange, the lateral surface of the central region of the pterygoid, the ventral, ventrolateral and ventromedial surfaces of the quadrate ramus of the pterygoid, the pterygoid ramus of the quadrate, and from the ventrolateral surface of the epipterygoid. No fibers arise from the posterodorsal surface of the pterygoid flange. The two portions run posteroventrally and slightly laterally and insert by means of fine tendons and fleshy attachments on the posteromedial surface of the mandible ventral to the adductor chamber and on the ventral and ventrolateral surfaces of the postcoronoid region of the mandible (Fig. 68A).

In Ctenosaura, the muscle has a similar pattern of origin and insertion to that in Sphenodon. It differs in that some fibers also originate from the basipterygoid process of the basisphenoid and the joint capsule separating the basisphenoid and pterygoid. The medially directed angular process and the well-developed retroarticular process provide more areas for its insertion in lizards.

The M. pterygoideus atypicus is a small tongue-shaped muscle in Sphenodon (Figs. 67A and 68A). As it is described by Gorniak et al. (1982), the muscle is characterized by its

Fig. 67. Ventral view of the M. pterygoideus typicus of <u>Sphenodon</u> <u>punctatus</u>.

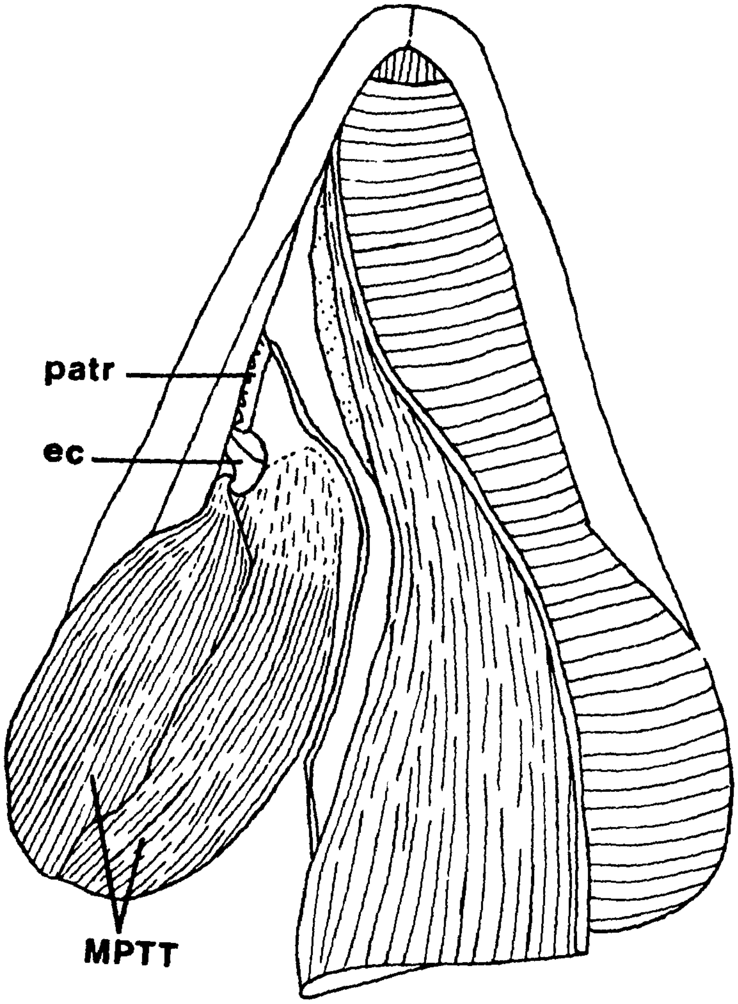
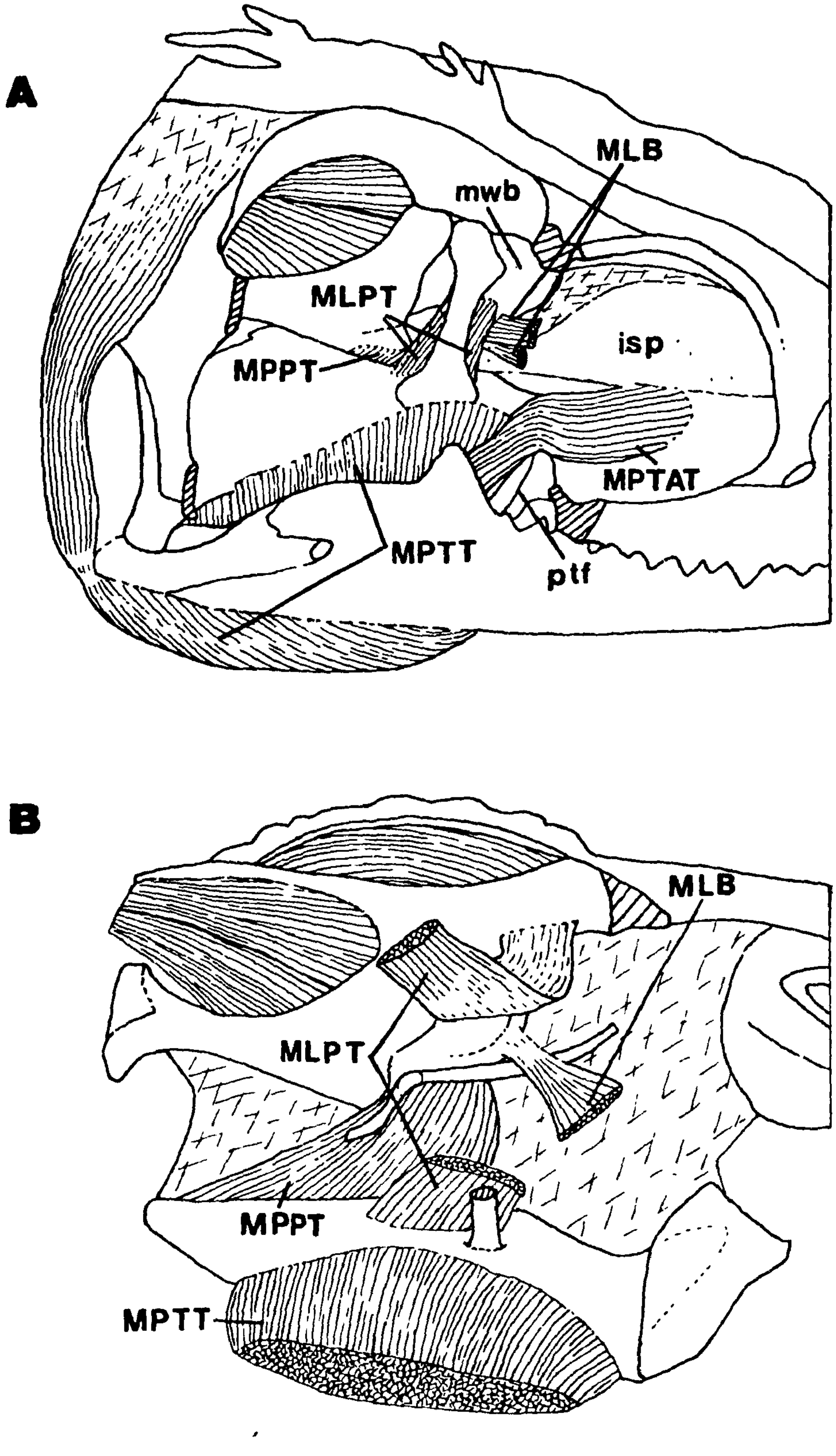

patr
ec
MPTT

Fig. 68. Lateral views of the deepest cranial muscles of A, Sphenodon punctatus and B, Ctenosaura pectinata (after Oelrich, 1956).


A
MLB
mwb
MLPT
isp
MPPT
MPTAT
MPTT
ptf
B
MLB
MLPT
MPPT
MPTT

sharp direction change. Its fibers originate from the posteodorsal surface of the palatine and the ventral margin of the interorbital septum. Its origin expands posteromedially to the dorsal surface of the anterior ramus of the pterygoid. Since the ectopterygoid forms a dorsally convex bridge-like brace between the maxilla and the palate, the fibers of the muscle extend posterodorsally anterior to the brace and then curve sharply downwards and slightly backwards along the posterodorsal surface of the pterygoid flange at about a 75° angle after passing the brace. In contrast with previous descriptions, the muscle clearly possesses two separate insertions. The lateral four-fifths of its fibers attach through a short but wide tendon to the posteroventral margin of the coronoid just anterodorsal to the adductor chamber, and the more medial fibers, via another small tendon, extend far posteroventrally and insert on the lower border of the adductor chamber at the level of the medial opening of the mandibular foramen (Fig. 77A).

M. adductor mandibulae posterior

The M. adductor mandibulae posterior in Sphenodon can be easily separated from the more lateral M. adductor mandibulae externus profundus by the more vertical orientation of its fibers. Between the M. adductor mandibulae posterior and the M. pseudotemporalis profundus is a conspicuous V-shaped gap through which pass the mandibular branch (V3) of the trigeminal nerve and the mandibular artery (Fig. 66A). The M.

adductor mandibulae posterior differs from that in previous studies in that the muscle arises from the lateral surface of the posterior process of the prootic just below the mandibular artery as well as from the posterodorsal surface of the pterygoid ramus of the quadrate. Its fibers insert by fine tendons and fleshy attachments to the dorsomedial border of the adductor chamber.

Gorniak et al. (1982) did not describe the M. adductor mandibulae posterior in their paper. However, their figure 1 clearly shows a muscle positioned posterior to the mandibular branch (V3) of the trigeminal nerve. This muscle was identified by them as the M. adductor mandibulae externus profundus, originating through two heads from the posterolateral and the anterolateral surfaces of the prootic and inserting on the posterior part of the medial surface of the basal aponeurosis. Their illustration of this muscle corresponds, in its topography and its relative position to the V3 branch of the trigeminal nerve, to the M. adductor mandibulae posterior but the writere's description corresponds to the M. adductor mandibular externus profundus in terms of its attachments, especially the insertion to the basal aponeurosis. It is possible that the description and illustration of these muscles have been confused in their paper.

In <u>Ctenosaura</u>, the fibers of the M. adductor mandibulae posterior arise primarily from the medial crest of the quadrate and extend more obliquely towards the insertion (Fig.

66B) because the pterygoid ramus of the quadrate is reduced.

b. Constrictor internus dorsalis

The M. constrictor internus dorsalis in Sphenodon can be subdivided into three muscles: the M. levator pterygoidei, the M. protractor pterygoidei and the M. levator bulbi. The last is well-developed and constant, but the first two are extremely variable (Ostrom, 1962; Haas, 1973) and need to be redescribed.

The M. levator pterygoidei in Sphenodon lies anterior, medial and posterior to the epipterygoid (Fig. 68A). Its fibers are a bit shorter than illustrated by Ostrom (1962) and originate from the ventrolateral surface of the membraneous wall of the braincase (Fig. 68A). It has not been reported that a string-like posterior tendon parallels the fibers of the muscle from the origin to insertion. The muscle fibers extend posteroventrally and attach mainly to the dorsal surface of the pterygoid; some lateral fibers insert on the ventromedial surface of the epipterygoid.

The M. protractor pterygoidei is also developed in Sphenodon, but it is much smaller and shows a different area of insertion than that described by Ostrom (1962). The muscle is overlapped anteriorly by the M. levator pterygoidei rather than being separated by a gap from the latter (Fig. 68A). Some fibers arise from the anterior inferior process of the prootic just posteroventral to the trigeminal notch. Some anterior fibers also come from the string-like posterior tendon of the M. levator pterygoidei. Its insertion is constricted to the dorsomedial surface of the quadrate ramus of the pterygoid close to its base.

In Ctenosaura, these two muscles are greatly developed in relation to the cranial kinesis exhibited by squamates. The M. levator pterygoidei originates from the ventrolateral margin of the parietal as well as from the membrane anterior to the prootic (Fig. 66B). The M. protractor pterygoidei is a large fan-shaped muscle forming the lateral wall of the middle ear cavity. It shows a complex origin from the inferior process of the prootic, the alar process of the basisphenoid and a tendon anterior to the prootic. Its fibers insert extensively on the dorsal border of the quadrate ramus of the pterygoid from the level of the epipterygoid to the level of the quadrate.

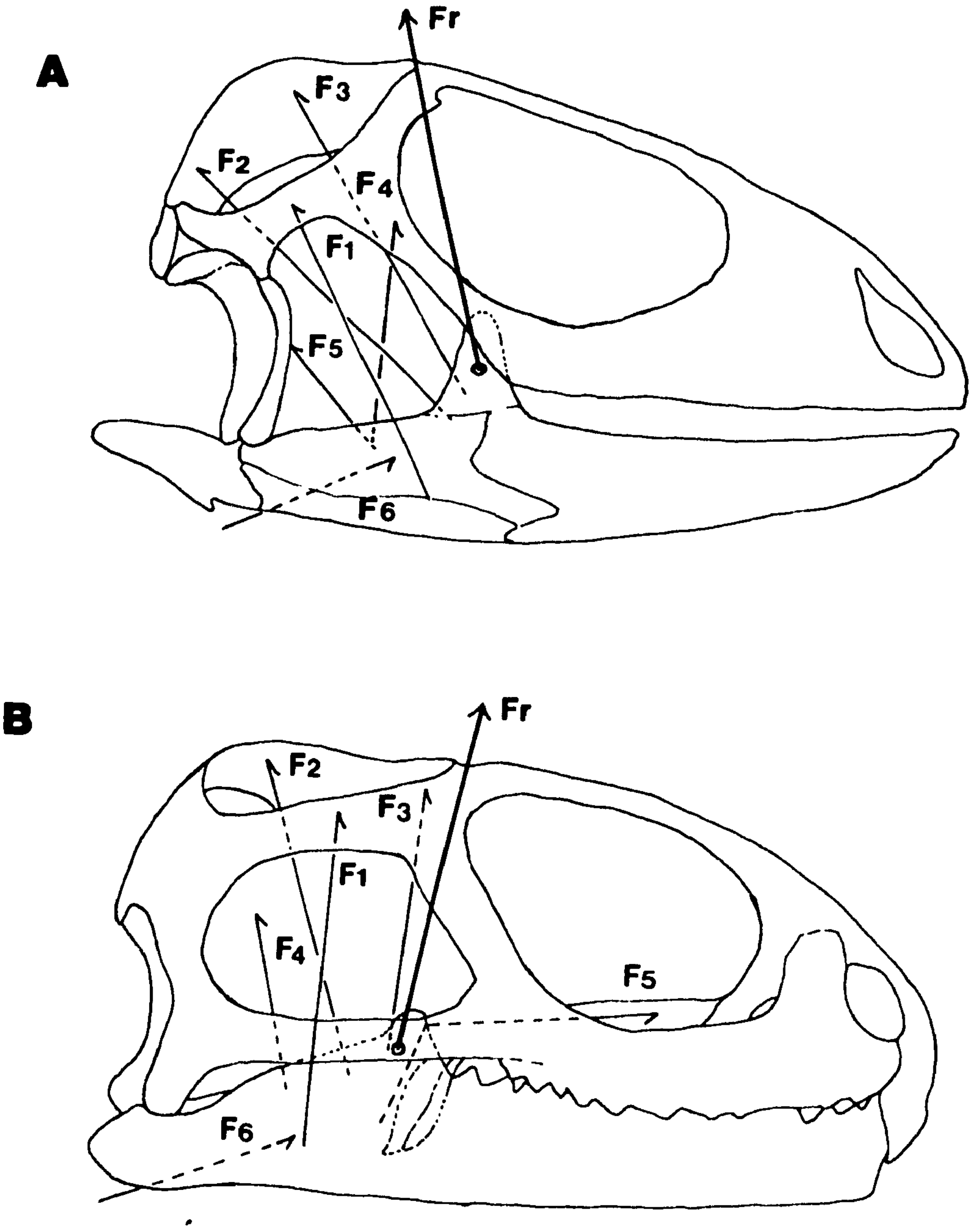
Anatomical Differences of Cranial Muscles Between Sphenodon and Lizards

It is evident from the above comparison that although the cranial muscles innervated by the trigeminal nerve in Sphenodon and lizards show a common pattern, there are numerous significant differences. The M. retractor anguli oris is clearly distinct from the M. levator anguli oris in Sphenodon, but it is absent in most lizards or only partially separated as a second origin of the M. levator anguli oris in a few genera such as Lanthanotus (Haas, 1973). All the adductor jaw muscles of Sphenodon, except for the M. pterygoideus typicus, display either a more vertical orientation or an otherwise differing orientation compared with their homologues in lizards. Perhaps the most significant difference is the presence of a separate M. pterygoideus atypicus in Sphenodon. Such an anterior subdivision of the M. pterygoideus has never been recorded in any squamate.

Haas (1973) argued that the presence of a separate M. levatores anguli oris and M. retractor anguli oris was a primitive condition in Sphenodon on the basis of the double origin of the M. levatores anguli oris in a few lizards and amphisbaenians.

Other than the M. pterygoideus typicus, only the M. pseudotemporalis profundus in Ctenosaura shows a posteroventral orientation. The others extend, at varying angles, in an anteroventral direction. The M. pseudotemporalis profundus is a relatively small muscle. It is assisted by the large mass (38.7% of the total weight of the adductor mandibulae in Varanus; Sinclair and Alexander, 1987) of the M. pterygoideus typicus, which also inserts at a small angle to the lower jaw. The sum of their forces directed anterodorsally is still much weaker than the joint forces of the other adductor muscles acting posterodorsally. Consequently, the resultant force of all the adductor jaw muscles acts posterodorsally (Fig. 69A). The correlative line of action has the same orientation as the long axis of the quadrate (Throckmorton, 1976; Bramble, 1978; Sinclair and Alexander,

Fig. 69. Diagrams of the approximate positions and directions of the adductor jaw muscles. A, an iguanid lizard: F1--MAME.Superficialis *sensu stricto*, F2--MAME.Medialis plus Profundus, F3--MPST.Superficialis, F4--MPST.Profundus, F5--MAM. Posterior, F6--MPT.Typicus, and Fr--The resultant force of all the adductors. B, *Sphenodon*: F1, F2, F6 and Fr have same meanings as their correspondents do in A; F3--MPST.Superficialis plus Profundus; F4--MAM.Posterior; and F5--MPT.Atypicus. In *Sphenodon* the estimated amount (N) of each force is derived from table 1 of Gorniak et al. (1982) and converted into percentage: 9.5% (F1), 23% (F2), 19.5% (F3), 17.1% (F4), 5.7% (F5), and 24.8% (F6). In vector analysis of the resultant force, the coronoid process was taken as the effort point of each force and the force amounts in the lizard are estimated based on those in *Sphenodon*. The length of the arrows in the figure are not proportional to the force of the individual muscles.


A
Fr
F3
F2
F4
F1
F5
F6
B
Fr
F2
F3
F1
F4
F5
F6

1987).

In Sphenodon, two additional posteroventrally oriented jaw muscles, the M. adductor mandibulae externus superficialis sensu stricto and the M. pseudotemporalis superficialis, plus the M. pseudotemporalis profundus and the M. pterygoideus typicus and atypicus comprise about 76.5% of the total wet weight of the adductor jaw muscles (Gorniak et al., 1982). The remaining three adductor muscles, the M. adductor mandibulae externus medialis, M. adductor mandibulae externus profundus and M. adductor mandibulae posterior are more vertical in orientation than their homologues in lizards. Consequently, the resultant force generated by all the adductor jaw muscles acts anterodorsally. Figure 69B shows the line of action of the result force that crosses the mandible at an angle of about 76 degree, approximately parallel to the direction of the long axis of the quadrate.

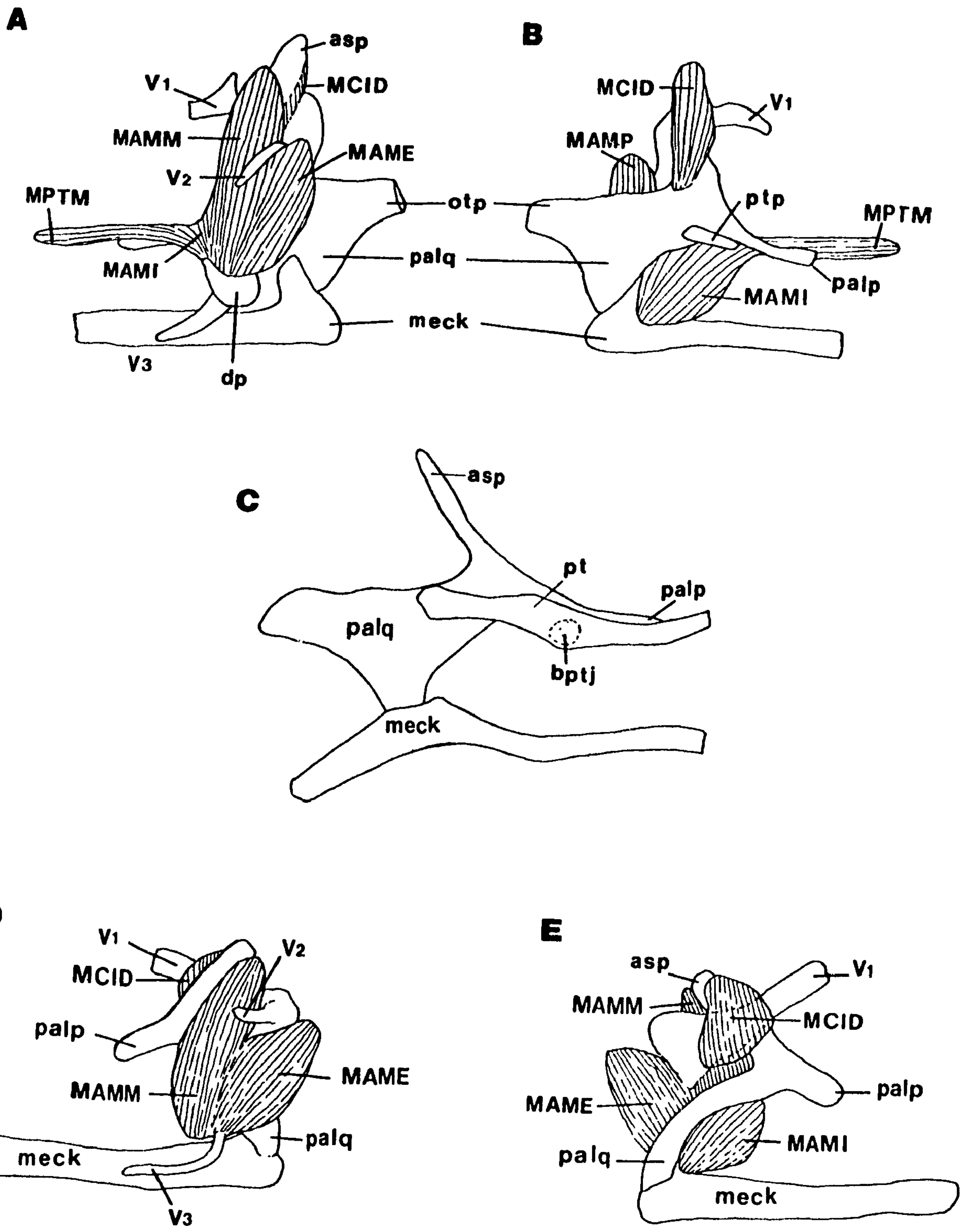
An anterior subdivision of the M. pterygoideus is a feature common to living reptilian groups other than squamates. It is as large as the posterior portion of the muscle in crocodiles (the M. pterygoideus anterior) or even larger in turtles (the M. pars rostro-medialis and the M. pars rostro-lateralis; Schumacher, 1973). The anterior subdivision has a similar origin and insertion in all groups. It arises from the dorsal surface of the palate in the orbital region: from the palatine, the anterior ramus of the pterygoid, and the interorbital septum in Sphenodon (Haas, 1973; Gorniak et al., 1982; this paper); from the walls of a groove formed by the pterygoid, palatine, the descending process of the parietal, the frontal and postfrontal in pleurodire turtle from the palatine, pterygoid, interorbital septum, maxilla, and the descending process of the prefrontal in crocodiles (Schumacher, 1973; Cong et al., submitted). As in Sphenodon, the fibers usually extend posteriorly first and then turn ventrally along the posterodorsal surface of the pterygoid flange and end by tendinous or fleshy attachments to the medial surface of the mandible just posteroventral to the coronoid process or anterior to the insertion of the M. adductor mandibular posterior.

In contrast, the posterior mass usually forms a large bulge at the posteroventral region of the head. Its origin is similar in all living reptiles, from bones around the subtemporal fenestra. The posterior mass never has its fibers arising from the dorsal surface of the palate. In Sphenodon and lizards, the posterior mass (the M. pterygoideus typicus) originates primarily from the anteroventral surface of the pterygoid flange, the lateral and ventromedial surface of the quadrate ramus of the pterygoid (in lizards) and the pterygoid ramus of the quadrate. In turtles, the posterior portion (the M. pars ventro-lateralis or plus the M. pars ventro-posterior; Schumacher, 1973) originates primarily from the free end of the trochlear process or the ventral surface of the pterygoid (if the trochlear process is absent) and the quadrate (if the M. pars ventro-posterior is present). In crocodiles, the posterior portion (the M. pterygoideus posterior; Schumacher, 1973; Cong et al., submitted) arises mainly by well-developed tendons or fibers from the anteroventral surface of the pterygoid flange. The posterior mass of the M. pterygoideus has the posteriormost insertion among adductor jaw muscles. It wraps around the posteroventral, posteromedial, and posterolateral surfaces of the mandible in Sphenodon, lizards and crocodiles. In turtles, the greatly reduced posterior portion inserts on the posteromedial tip of the lower jaw.

I suggest that the M. pterygoideus atypicus of Sphenodon is most probably homologous either with the M. pterygoideus anterior of Crocodiles or with the M. pars rostro-medialis (plus the M. pars rostro-lateralis in some members) of turtles based on their topographies, constant origin and insertion. Meanwhile, the M. pterygoideus typicus of Sphenodon is homologous with the M. pterygoideus typicus of lizards, the M. pterygoideus posterior of crocodiles, and the M. pars ventro-lateralis or this muscle plus the M. pars ventro-posterior of turtles. This argument can be further supported by evidence from embryonic development.

Edgeworth (1931 and 1935) first noticed that after the separation of the M. adductor mandibulae externus and internus from the M. adductor mandibulae medialis, a slender fasciculus, the M. pterygo-mandibularis grows forwards from the anterior end of the M. adductor mandibulae internus at embryonic stage PQ of Sphenodon (Fig. 70A, B). It extends at first on the outer side and then above the palatal process of

Fig. 70. Embryos of Sphenodon punctatus (A, B and C) and Lacerta muralis (D and E) illustrating relationships between the adductor jaw muscles and the cranial structures (after Edgeworth, 1935). A, Lateral (anterior to left) and B, Medial (anterior to right) views of the left side in stages P--Q; C, Medial view of the Platoquadrate, Meckel's cartilage and pterygoid in stage R (anterior to right); D, lateral (anterior to left) and E, medial (anterior to right) views of the left side at 5 mm.


A
asp
V1
MCID
MAMM
MAME
V2
MPTM
otp
MAMI
palq
meck
V3
dp
B
MCID
V1
MAMP
otp
ptp
MPTM
palq
palp
MAMI
meck
C
asp
pt
palp
palq
bptj
meck
D
V1
V2
MCID
palp
MAME
MAMM
palq
meck
V3
E
asp
V1
MAMM
MCID
palp
MAME
MAMI
palq
meck

the palatoquadrate and arises far forwards (beyond the anterior end of the palatal process) from the dorsal surface of the palate arcade in stage R (Fig. 70C). Edgeworth concluded that the muscle was homologous with the large portion D of the M. adductor mandibulae internus of Crocodiles (his fig. 585b, 1935) and with dorsal fibers of the adductor mandibulae internus of the Chelonia. As early as 1926, Lakjer described the homologous fibers of the muscle in Varanus. These fibers or muscles in reptiles other than Sphenodon also show a far anterior origin from the dorsal surface of the palate during development--from the pterygoid in Varanus, from the maxilla, palatine and pterygoid in crocodiles, and from the palatine and the base of the interorbital septum in the Chelonia (Edgeworth, 1935). However, from the illustrations of Edgeworth, lizards other than Varanus do not have an anterior extension of the M. adductor mandibulae internus after complete subdivision of the three masses of the M. adductor mandibulae during embryonic development (Fig.70D, E). Based on the anterior position and the similar origin from the dorsal surface of the palate, the M. pterygo-mandibularis of Edgeworth in the embryo of Sphenodon should be homologous with the M. pterygoideus atypicus in adults. If this were true, the M. pterygoideus typicus may not have been separated yet from the M. adductor mandibulae internus when the M. pterygoideus atypicus first become distinct in the early development of Sphenodon. On the basis of its embryology, the M. pterygoideus atypicus in Sphenodon and its homologues in crocodiles and turtles may be a primitive subdivision of the adductor jaw muscles. On the other hand, the absence of the M. pterygoideus atypicus in lizards most probably indicates a derived condition among the lepidosauromorphs.

Relations Between the Adductor Jaw Muscles and Associated Bony Structures

The differences in the adductor jaw musculature of Sphenodon and lizards are presumably correlated with different patterns of the bony structures in the temporal region.

a. The M. levator anguli oris (including the M. retractor anguli oris) varies between Sphenodon and lizards, but it has no insertion on any bony structure. This muscle was probably not influenced by the changes of the bony structure of the temporal region.

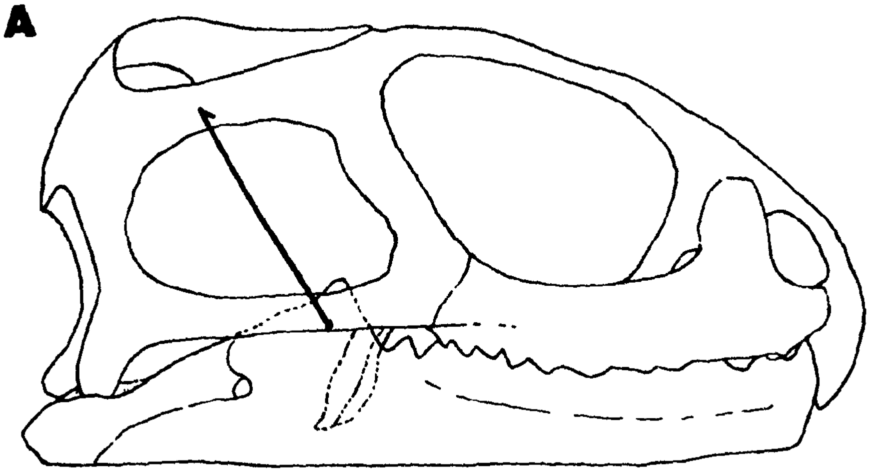
b. The temporal region is longer relative to the skull length in Sphenodon (about 41.5%) than in common iguanid lizards (about 32.5%). A relatively long temporal region means that the centre of origin of the adductor jaw muscles (not including the M. pterygoideus) is relatively anterior in position. The temporal region is short relative to skull length in iguanid lizards which indicates a relatively posteriorly located centre of origin. However, the area for insertion of the adductor jaw muscles between the coronoid process and the quadrate is relatively long--reaching about

41.3% of the mandible length, compared with about 45.3% in Sphenodon. It is obvious that the centre of insertion is relatively anteriorly situated in both Sphenodon and iguanid lizards. If we take the coronoid process as the insertion centre and the midpoint of the temporal region as the centre of origin, the distance between the projection of the centre of origin on the mandible and the centre of insertion is greater in iguanid lizards than in Sphenodon (Fig. 71). This greater difference between the two centres leads to a more anteroventral orientation of each adductor jaw muscle (except for the M. pterygoideus) in lizards.

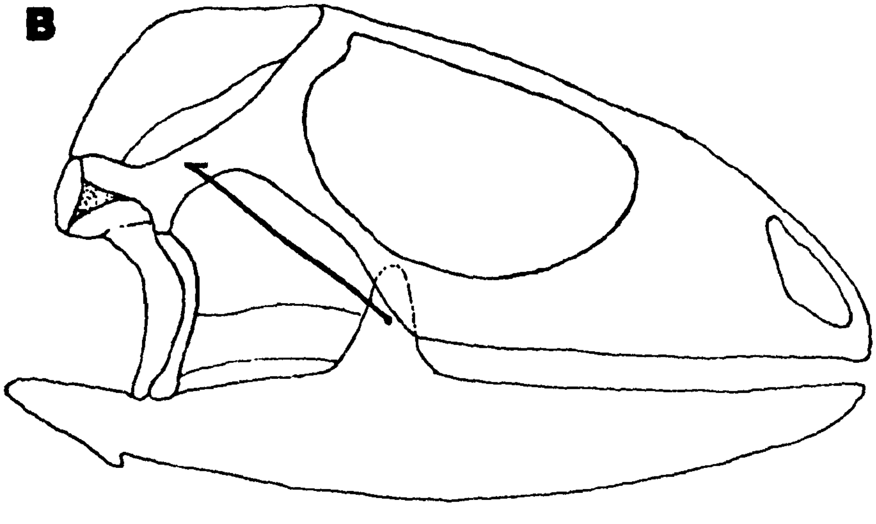
c. The M. pterygoideus has an anterior subdivision, the M. pterygoideus atypicus, in Sphenodon as in crocodiles and turtles. As described above, the M. pterygoideus atypicus extends first posteriorly and then turns ventrally against the posterodorsal surface of the pterygoid flange. It is obvious that the flange functions as a trochlea to help the M. pterygoideus atypicus change the acting direction. The trochlear function of the pterygoid flange has been demonstrated in turtles and crocodiles (Schumacher, 1973; Cong et al., submitted). Because the pterygoid flange receives an extra force generated by the M. pterygoideus atypicus, it must become stronger and larger in animals with the muscle than in animals without the muscle. In other words, the more massive the M. pterygoideus atypicus is, the larger the pterygoid flange is. Crocodiles have a very large anterior subdivision of the M. pterygoideus so that they have a huge pterygoid

Fig. 71. Lateral views of the skulls of A, *Sphenodon* and B, an iguanid lizard showing the approximate direction of the resultant force of major adductor jaw muscles (except for the M. pterygoideus).

A



B



flange (Fig. 72A, B). This is also true in turtles where a large pterygoid flange (the trochlear process of the pterygoid) is in direct proportion to a massive anterior portion of the M. pterygoideus (Schumacher, 1973).

Since the M. pterygoideus atypicus and its homologues in other reptiles run, in common with the other adductor jaw muscles, through the subtemporal fenestra posterior to the palate, the ratio of the area of the pterygoid flange to the fenestra (Fig.73) can be used as an index for estimating the probable size of the muscle in different animals, especially in fossil forms. In Sphenodon the M. pterygoideus atypicus has a very small mass, occupying only about 2.2% of the total wet weight of all the adductor jaw muscles or 5.1% of the total wet weight of the M. pterygoideus (Gorniak et al., 1982). It seems unlikely that such a small proportion is able to make a significant influence on the pterygoid flange. The flange (Fig. 72C) is relatively much smaller than that of crocodiles and comparable to the size in Ctenosaura. Squamates do not have the M. pterygoideus atypicus and the pterygoid flange is greatly reduced (Fig. 72D, E).

d. Sphenodon has a complete lower temporal bar in contrast with the condition in lizards in which the lower temporal bar is completely lost. It has been suggested (Rieppel and Gronowski, 1981) that the reduction of the lower temporal bar within diapsids is correlated to the development of the posteroventral portion of the M. adductor mandibulae externus superficialis sensu stricto. This portion expanded

Fig. 72. Ventral views of the skulls of modern diapsid reptiles. A and B, Alligator, displaying a massive anterior part of the M. pterygoideus and a relative large pterygoid flange. C, Sphenodon; D, an iguanid lizard; and E, an agamid lizard; showing a relatively much smaller pterygoid flange. A and B after Schumacher (1973); D and E after Gauthier et al. (1988).

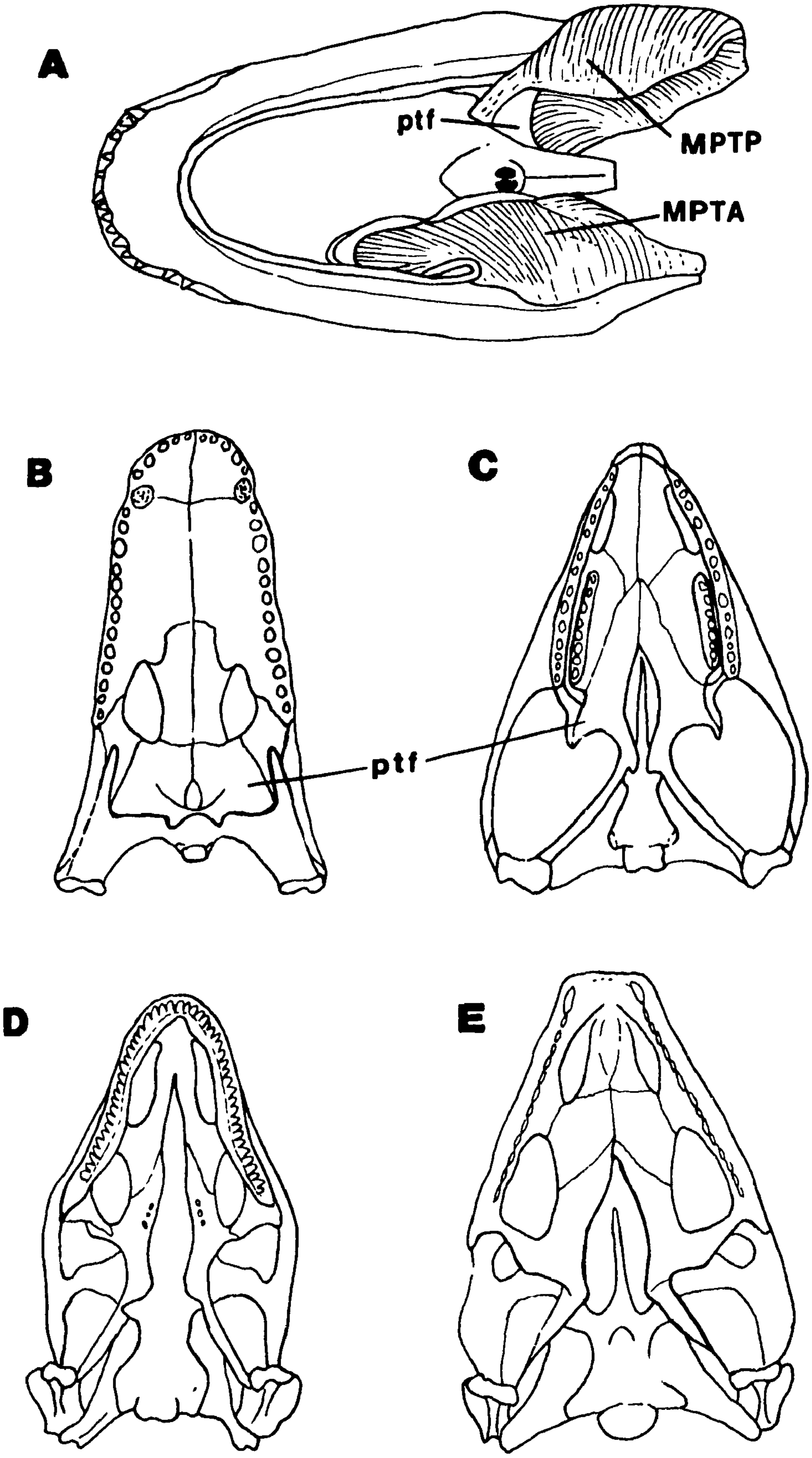
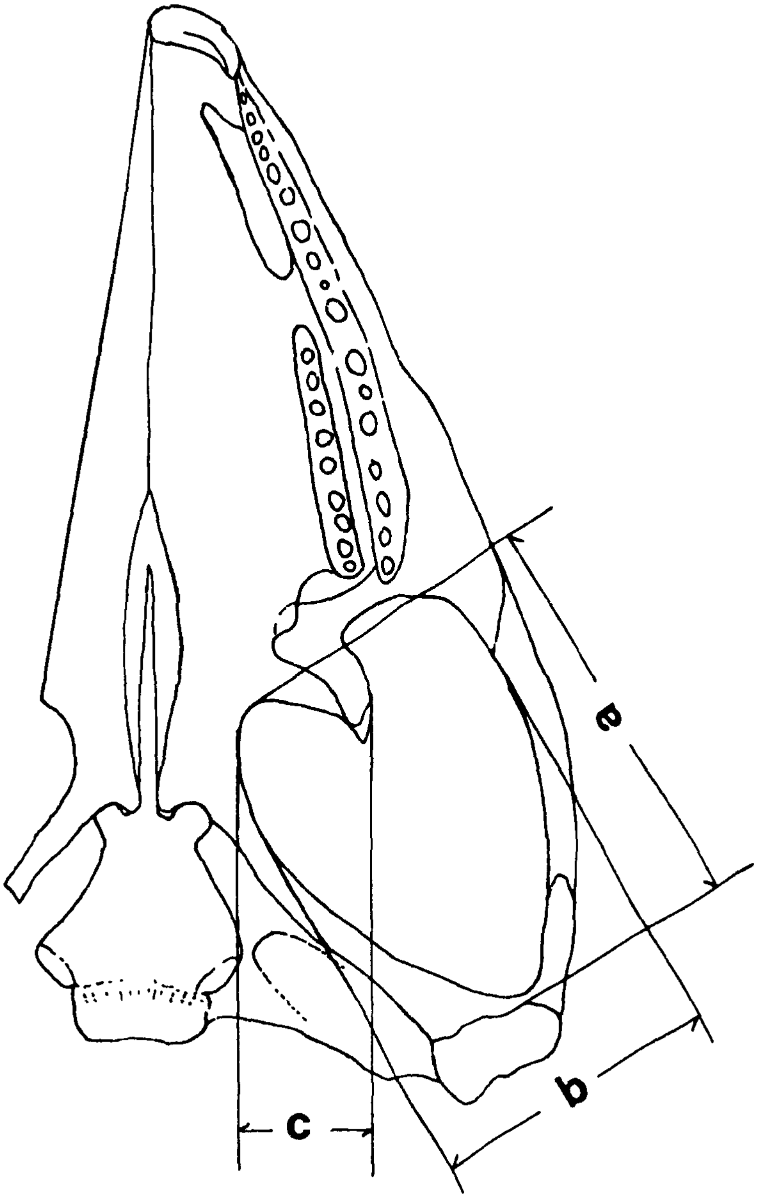

A
ptf
MPTP
MPTA
B
C
ptf
D
E

Fig. 73. Ventral view of the left half of the skull of Sphenodon illustrating how measurements of the pterygoid flange and the subtemporal fenestra were made. The ratio of the pterygoid flange to the subtemporal fenestra = C/[(a + b)/2].


a
b
c

ventrolaterally, escaping from the original confines of the lower temporal bar and inserted on the lateral surface of the mandible. Although the lower temporal bar is complete in *Sphenodon*, the M. adductor mandibulae externus superficialis *sensu stricto* closely resembles that of *Ctenosaura*. Since the lower temporal bar bows laterally beyond its original limit in *Sphenodon*, the lateral fibers of the M. adductor mandibulae externus superficialis *sensu stricto* can still expands laterally and insert on the lateral surface of the mandible. Whiteside (1986) reasoned that a complete lower temporal bar was secondarily developed in the Sphenodontida. If this were the case, an incomplete lower temporal bar and a lateral portion of the M. adductor mandibulae externus superficialis that inserted on the lateral side of the mandible would have been primitive for the group. A redeveloping lower temporal bar would have to bow laterally and extend outside the muscle, which seems true in most, if not all, sphenodontidans (Fraser, 1988).

e. A streptostylic quadrate has long been considered a major difference between lizards and the other reptiles. With a mobile quadrate, lizards are able to move their mandible forwards and backwards through rotation of the quadrate with its dorsal articulation. Despite a fixed quadrate, the mandible of *Sphenodon* can also make propalinal movements by sliding at the jaw articulation (Robinson, 1976; Gorniak et al., 1982).

A quadrate that is mobile relative to the rest of the skull has been postulated in many fossil diapsids with and without a lower temporal bar (Walker, 1961, 1972; Ewer, 1965; Cruickshank, 1972; Gow,1975; Evans, 1980), but the presence of a descending process of the squamosal and an overlap between the rami- of the quadrate and pterygoid in non-squamates indicate that the degree of the movement was restricted in comparison with that in squamates. Therefore, only the quadrate of the Squamata is considered to be truly streptostylic.

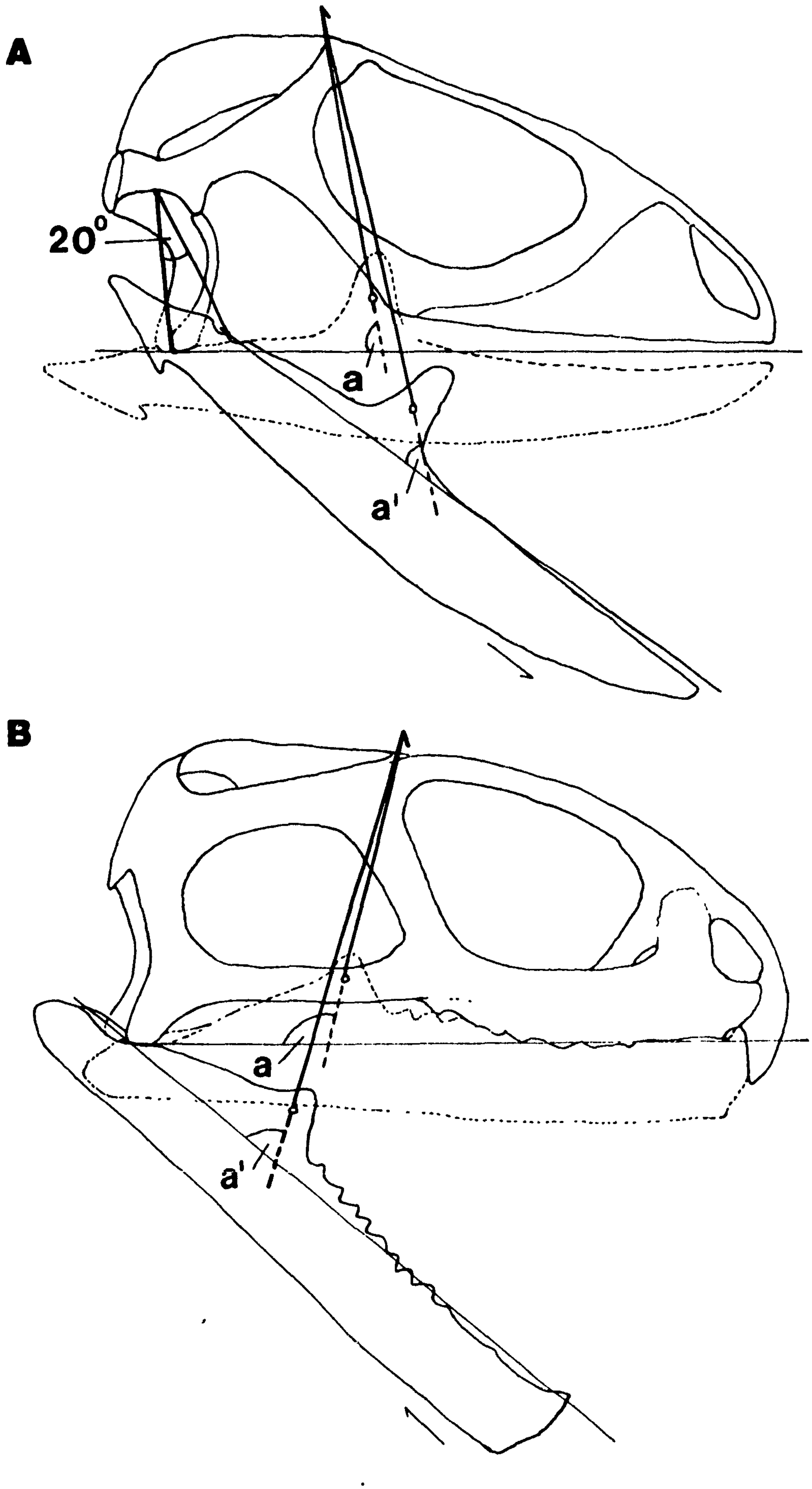
In lizards, ligaments binding the quadrate to the quadrate ramus of the pterygoid medially and connecting the quadrate and jugal laterally (Throckmorton, 1976; Smith, 1982) restrict the posterior movement of the quadrate at the beginning of the jaw cycle. Recently, using cinematic, cineradiographic and electromyographic techniques, the feeding apparatus of Uromastyx, a herbivore, (Throckmorton, 1976) and Varanus, a carnivore, (Smith, 1982) have been studied. In both lizards the distal end of the quadrate moves forward during jaw opening and backward during jaw closing so that the mandible first protracts and then retracts. However, propalinal movement in Sphenodon is more complex and has a reverse relationship to the adduction-abduction cycle: sliding posteriorly during jaw opening, partially anterior during jaw closing and further anterior when the jaws are fully closed (during the shearing phase; Gorniak, et al., 1982).

As pointed out earlier, the resultant force of all the adductor mandibulae muscles adduct posterodorsally in lizards

(Bramble, 1978; Throckmorton, 1976; Sinclair and Alexander, 1987), leading to a posterodorsal movement of the mandible during jaw closure. On the contrary, the joint forces of all the adductor mandibulae muscles act anterodorsally, pulling the mandible upward and forward in Sphenodon.

The anterior movement of the mandible during jaw opening in lizards results in the more anterior position of the centre of insertion so that the insertional angle of each adductor jaw muscle is reduced (Fig. 74A), altering the relative magnitude of each moment arm. The posterior retraction of the mandible relative to the quadrate during jaw opening in Sphenodon also leads to a decrease rather than an increase of the insertional angle of each adductor jaw muscle. Since the resultant force acts in an opposite direction to that in lizards, the posterior retraction has a different effect on jaw mechanics in Sphenodon. If we assume a maximal gape angle of 35° (based on figure 5B; Gorniak et al., 1982) and an anterodorsally directed resultant force at an angle of about 76° (see above), the posterior retraction of the mandible during jaw opening would greatly influence the acting direction of the resultant force, i.e. it would change from anterodorsal to posterodorsal relative to the mandible (Fig. 74B). That is why little protraction of the mandible has been recorded during early stages of jaw closing but does occur when the jaws are closed or nearly closed (Gorniak et al., 1982).

Fig. 74. Diagrams showing the decrease of the insertional angles (from a to a′) of the adductor jaw muscles during jaw opening in A, an iguanid lizard and B, *Sphenodon*. Thick lines represent direction change of the resultant force of all the adductors relative to the mandible.


A
20°
a
a'
B
a
a'

Adductor Jaws Musculature in Primitive Sphenodontidans

In comparison with derived genera (such as Clevosaurus, Brachyrhinodon, Asiacephalosaurus, Rarojugalosaurus, Dianosaurus and etc.), the living Sphenodon and squamates, the most primitive sphenodontidans, Gephyrosaurus and Diphydontosaurus, are distinct in the following aspects: the temporal region and the post-coronoid area are relatively shorter, about 1/3 of the skull or mandible length (Table 3); the lower temporal bar is incomplete and bows laterally to a much lesser degree; and the ratio of the pterygoid flange to the subtemporal fenestra is relatively higher (more than 50%). With these features in mind, one can make a plausible restoration of a pattern of the adductor jaw musculature, provided that all three major units of the M. adductor mandibulae in the fossil forms had the same relative position as in the living Sphenodon and lizards.

A short temporal region indicates a relatively posterior centre of origin of the adductor jaw muscles while a short postcoronoid area means an insertion centre (the coronoid process) relatively close to the jaw articulation. This similarity in position of the original and insertional centres is comparable to the situation seen in Sphenodon (in which the temporal region and the insertion area both reach more than two-fifths of the skull or mandible lengths; Fig. 75) and indicates a similar orientation of the adductor jaw muscles. However, in the two primitive sphenodontidans, the relatively

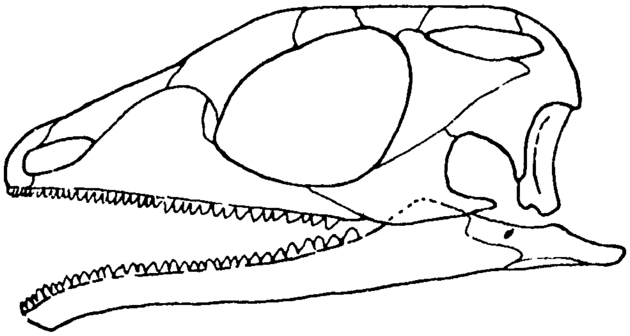
Table 3. Major ratios* between parts of skull [*Youngina*, *Ctenosaura* (a iguanid lizard) and selected sphenodontidans]

		POR/SL	INR/ML	PTFL/STPF
1	*Youngina*	28.7	38.8	56.7
2	*Ctenosaura*	32.5	41.3	----
3	*Gephyrosaurus*	34.9	35.0	50.6
4	*Diphydontosaurus*	30.4	33.3	50.1
5	*Planocephalosaurus*	30.6	42.5	41.4
6	*Palaeopleurosaurus*	40.7	39.5	41.7
7	*Brachyrhinodon*	48.1	47.4	45.7
8	*Clevosaurus*	40.9	44.7	45.9
9	*Asiacephalosaurus*	41.0	42.5	40.4
10	*Rarojugalosaurus*	40.1	40.5	43.0
11	*Homoeosaurus*	28.5	38.2	39.7
12	*Sphenodon*	41.5	45.3	37.7

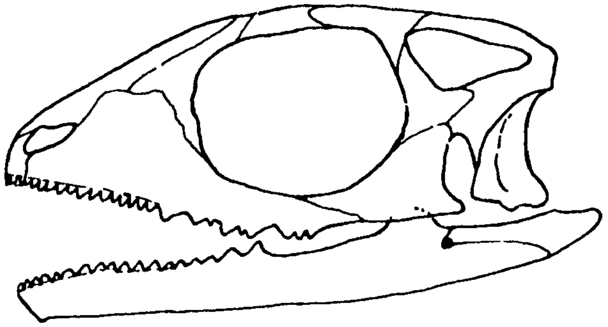
*--All the ratios are multiplied by 100. POR--The postorbital region from the posterior border of the orbital to the posterolateral edge of the squamosal; SL--The skull length from the snout to the posterolateral edge of the squamosal; INR--The insertional region of the adductor jaw muscles from the anterior edge of the coronoid process to the posterior margin of the articular fossa; ML--The mandible length from the synthesis to the posterior edge of the articular fossa; PTFL--The width of the pterygoid flange (see figure 73); STPF -the average of the maximum length and width of the subtemporal fenestra (See figure 73). Data in 1 and 3-8 are based on figures: 1, from Carroll, 1988a; 3, from Evans, 1980; 4, from Whiteside, 1986; 5, from Fraser, 1982; 6, from Carroll, 1985; 7, from Fraser & Benton, 1989; and 8, from Fraser, 1988.

Fig. 75. Lateral views of the skulls of the primitive sphenodontidans. A, Gephyrosaurus (after Evans, 1980); B, Diphydontosaurus (after Whiteside, 1986); and C, the living Sphenodon; illustrating that the temporal and postcoronoid regions are relatively shorter in the two primitive genera.

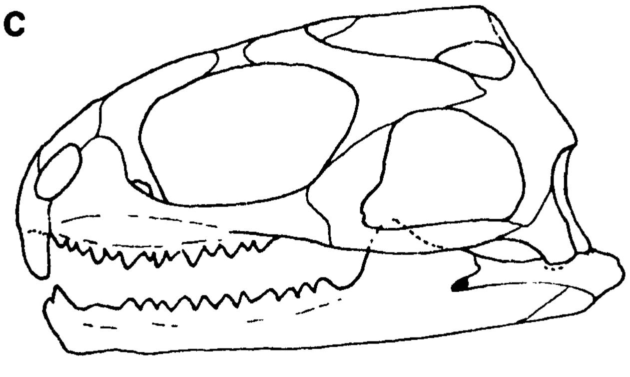
A



B



C



short temporal region indicates a relatively small mass and a limited intrinsic strength of the adductor jaw musculature while an insertion region close to the jaw articulation indicates a relatively short moment arm. The adductor jaw muscles with a short moment arm can make fast but weak bites. This is probably suited to their pleurodont or partially pleurodont dentition (Robinson, 1973).

The incompleteness and lateral bowing of the lower temporal bar of *Gephyrosaurus* and *Diphydontosaurus* suggest that the lateral portion of the M. adductor mandibulae externus superficialis *sensu stricto* could have extended laterally to insert on the lateral surface of the mandible. However, the lateral portion of the muscle in these two genera could not have been as large as it is in *Sphenodon* and lizards in which the lower temporal bar either bows greatly laterally or is completely lost.

As argued above, the size of the pterygoid flange is in direct proportion to the mass of the M. pterygoideus atypicus in extant reptiles. The ratio of the area of the flange to that of the subtemporal fenestra is much higher in *Gephyrosaurus* and *Diphydontosaurus* than in *Sphenodon* (Table 3). This suggests that these two primitive genera had a relatively massive M. pterygoideus atypicus.

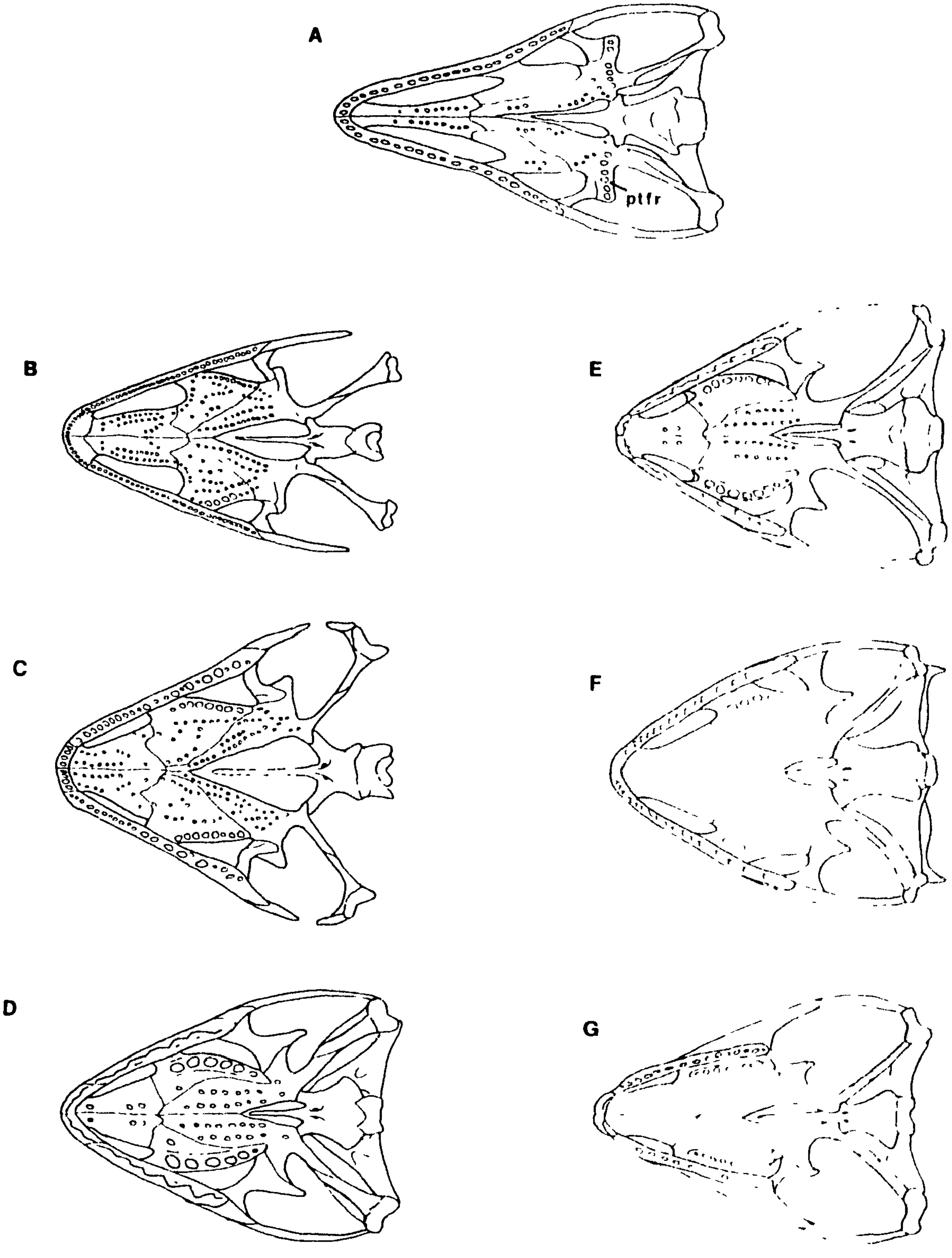
Reduction of the M. Pterygoideus Atypicus

It has been demonstrated that the M. pterygoid atypicus is a primitive subdivision of the M. adductor mandibulae internus in reptiles and that it may have been relatively massive in primitive sphenodontidans. The small-sized M. pterygoideus atypicus in the living Sphenodon and the absence of this muscle in squamates reasonably suggests reduction within the Lepidosauria. The reduction of the M. pterygoideus atypicus within the Sphenodontida can be inferred by the decreasing ratio of the pterygoid flange to the subtemporal fenestra (Fig. 76 and Table 3). According to this ratio, the genera Clevosaurus, Asiacephalosaurus, and Homoeosaurus must have had a M. pterygoideus atypicus with a mass relatively smaller than that of the primitive forms Gephyrosaurus and Diphydontosaurus but relatively larger than that of the living Sphenodon. Therefore, a massive M. pterygoideus atypicus or the anterior portion of the M. pterygoideus should be theoretically expected in the common ancestor of the Sphenodontida and Squamata.

Youngina, known from well-preserved specimens, is usually considered a representative of primitive lepidosauromorphs (Evans, 1984; Benton, 1985; Carroll, 1988a). Its pterygoid flange is relatively larger (Fig. 76A) than in the most primitive sphenodontidans Gephyrosaurus and Diphydontosaurus, indicating the presence of a relatively more massive anterior portion of the M. pterygoideus.

It is probable that a massive anterior portion of the M. pterygoideus was closely correlated to a feeding method employed by primitive lepidosauromorphs. As in other early

Fig. 76. Ventral views of the skulls of A, Youngina (after Carroll, 1988a); B, Gephyrosaurus (after Evans,1980); C, Diphydontosaurus (after Whiteside, 1986); D, Clevosaurus (after Fraser, 1988); E, Asiacephalosaurus; F, Homoeosaurus; and G, Sphenodon; showing a reduction of the pterygoid flange.


A
ptfr
B
E
C
F
D
G

diapsids, Youngina had a pterygoid flange equipped with a transverse row of large pterygoid teeth along the ventral margin of the anteroventral surface. This row of large teeth may have served to hold active prey. Since the anterior portion of the muscle runs ventrally along the posterodorsal surface of the flange, it would have had, with the assistance of the trochlear flange, a good mechanical advantage for producing a strong adducting force (Fig. 68A). On the other hand, the lower temporal bar was complete and could not have bowed laterally to any degree, leaving no room for the development of any laterally positioned subdivision of the M. adductor mandibulae externus superficialis to add force to the bite. The dorsal mass of the adductor jaw musculature was greatly restricted not only by the lower temporal bar but also by a relatively short temporal region (slightly more than 1/4 of the skull length). It may not have been able to generate a force strong enough to hold active prey. It was therefore necessary for the anterior portion of the M. pterygoideus to have a large mass in the early lepidosauromorph.

The reduction of the M. pterygoideus atypicus in the Sphenodontida was possibly related to the loss of the transverse row of large pterygoid teeth in all known genera, indicating some change in feeding mechanism. With the posterior break and lateral bowing of the lower temporal bar, the dorsal part of the adductor jaw musculature would be able to develop additional mass and insert on the lateral surface of the mandible. In comparison with the M. pterygoideus atypicus, the dorsal mass has a better mechanical advantage to generate adducting force without relying on any additional bony structure to alter the acting direction of the muscle. This advantage may have led to further decrease of the mass of the M. pterygoideus atypicus in the group.

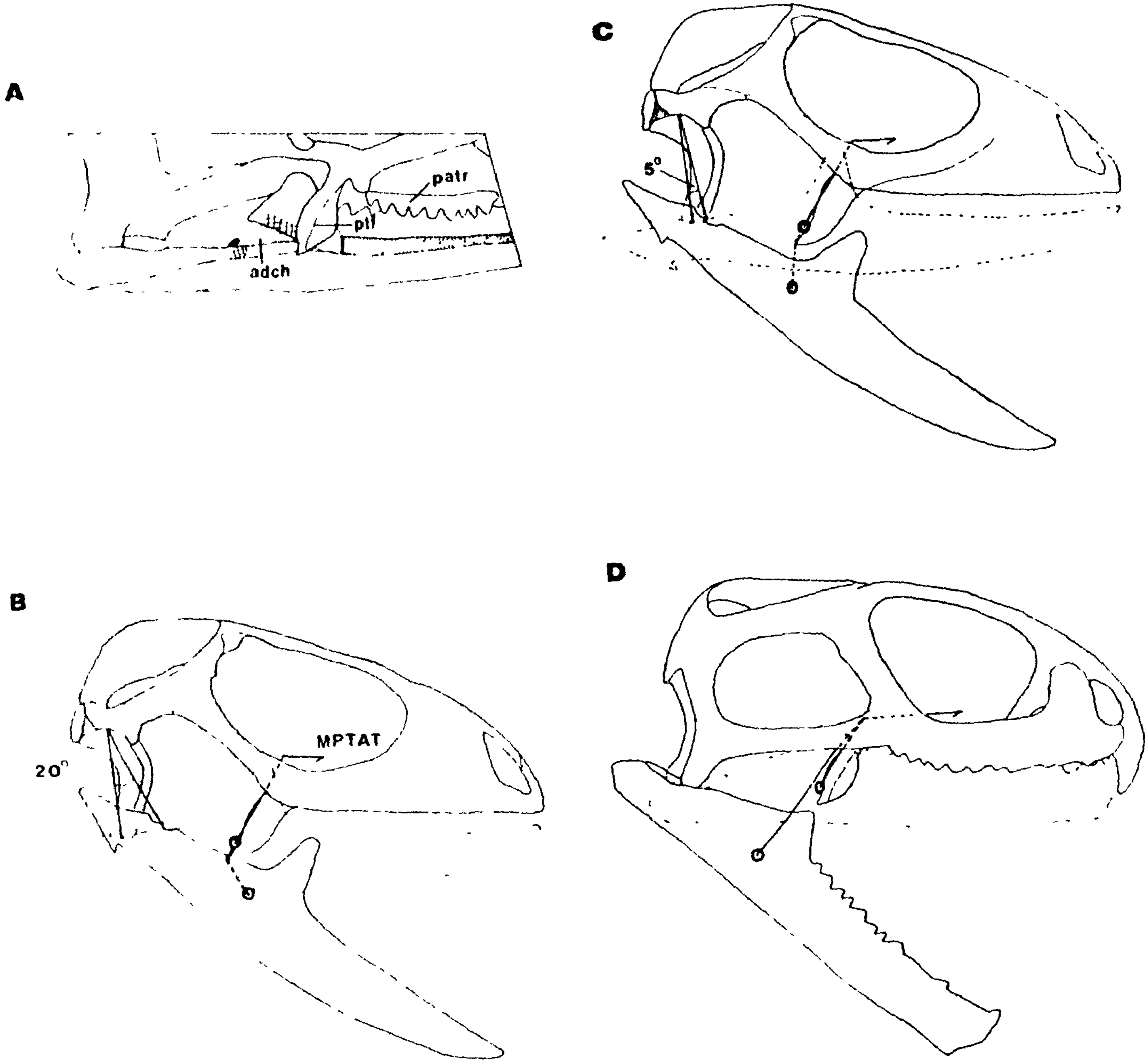
In the living Sphenodon, the feeding method has greatly changed relative to primitive sphenodontidans. The propalinal movement of the mandible needs a strong translational force. The posterior portion of the M. pterygoideus, the M. pterygoideus typicus, is oriented so that it is able to produce a very strong horizontal force. The muscle becomes relatively more massive in comparison with other extant reptiles, reaching 41.4% of the total wet weight of all the adductor jaw muscles (Gorniak et al., 1982). The growth of the M. pterygoideus typicus appears to have resulted in a reduction of the more anterior jaw adductor, the M. pterygoideus atypicus, which is remarkably small in Sphenodon. No matter how tiny it is, the muscle has been retained throughout the history of the Sphenodontida.

The complete absence of the M. pterygoideus atypicus in the Squamata shows a qualitative difference from the situation in the Sphenodontida. This may have been closely associated with the development of a streptostylic quadrate, which greatly effects the feeding mechanism.

The mandible moves anteroventrally during jaw opening in squamates. The anterior shift of the mandible results in the anterior movement of the insertional area of each adductor muscle. This causes changes in the insertional angle of most adductor jaw muscles. This shift would most strongly effect the M. pterygoideus atypicus if that muscle were present and inserted on an area similar to that in Sphenodon.

The M. pterygoideus atypicus inserts primarily on the posteroventral margin of the coronoid bone along the anterodorsal border of the adductor chamber where the thickened lateral side of the pterygoid flange braces the coronoid process. Its ventral tip is lower than the muscle insertion site when the jaws are closed (Fig. 77A). It is evident from such a geometry that the M. pterygoideus atypicus would block the movement of the jaw relative to the pterygoid flange if the quadrate moves forward as the jaws open. It is possible that when the jaws open, the insertion site of the muscle drops down to a lower position; the mandible could move forward with the protraction of the quadrate. However, another problem would arise when the muscle had to bend forwards around the ventral edge of the pterygoid flange (Fig. 77B). Since muscle fibers cannot be stretched beyond about 30% of their relative length (Liem, 1977), the M. pterygoideus atypicus could not stretch enough to compensate for its movement around the pterygoid flange without decreasing the gape of the mouth. Even if the quadrate moved forward only 5° and the mouth opened at an angle of 35°, this problem could not be avoided (Fig. 77C). It has been recorded that the quadrate is able to move forwards about 14° in Iguana and 30° in Uromastyx (Throckmorton, 1976). Consequently, the presence

Fig.77. Diagrams of the geometrical changes in the M. pterygoideus atypicus during the jaw cycle in *Sphenodon* and a lizard (if the muscle were present). A, Medial and slightly dorsal view of the mandible of *Sphenodon* with the pterygoid flange occluded, showing the relationship of the insertional sites (cross hatching) of the muscle with the pterygoid flange when jaws are closed. B and C, an iguanid lizard, displaying impossibility of anterior movements of the mandible at the beginning of jaw opening if the M. pterygoideus atypicus were present and anterior bending of the muscle around the pterygoid flange when the quadrate protracts anteriorly during jaw opening. D, *Sphenodon*, illustrating the M. pterygoideus atypicus during jaw opening in which the mandible retracts posteriorly.


A
patr
ptf
adch
B
20°
MPTAT
C
5°
D

of the M. pterygoideus atypicus would make the anterior movement of the quadrate almost impossible during jaw opening in squamates. In contrast, the mandible moves posteroventrally during jaw opening in Sphenodon, which increases rather than reduces the functional advantage of the M. pterygoideus atypicus (Fig. 77D).

From these arguments, the question as to whether a mobile or a fixed quadrate has been retained from the common ancestor of the Sphenodontida and Squamata should be clear: the streptostylic quadrate is a derived condition within the Lepidosauria. The dichotomy of the Sphenodontida and the Squamata could not have occurred after the origin of the streptostylic quadrate unless the M. pterygoideus atypicus had re-evolved in sphenodontidans.

Retention of the Fixed Quadrate in the Sphenodontida

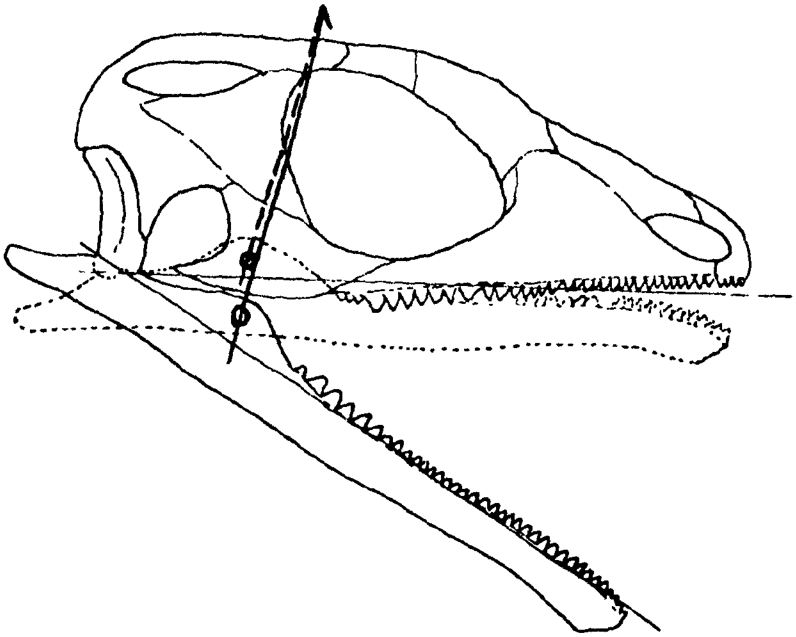
Extending the incipient shearing action in the most primitive sphenodontidan, Gephyrosaurus, precise tooth occlusion was further developed in Diphydontosaurus, as indicated by strong wear facets on the lateral aspects of the posterior acrodont teeth of the dentary (Whiteside, 1986). This trend was reinforced in more derived genera with fully acrodont dentition, such as Clevosaurus, Asiacephalosaurus and Rarojugalosaurus. It would appear likely that a mobile quadrate would mechanically effect the precision of occlusion. However, Uromastyx (an agamid lizard) with an acrodont dentition has a precise tooth occlusion, although its quadrate is fully streptostylic (Robinson, 1976; Throckmorton, 1976). This apparent contradiction between the early sphenodontidans and Uromastyx is not difficult to understand when the differences in their adductor jaw musculature are considered.

As in other lizards, the resultant force of all the adductor jaw muscles acts posterodorsally in Uromastyx (Haas, 1973; my dissection) and the line of action remains anteroventrally oriented with a lesser angle during jaw opening (Fig. 74A). The streptostylic quadrate in lizards is bound by two ligaments, one between its medioventral end and the quadrate ramus of the pterygoid and a second between its lateroventral end and the posterior tip of the jugal (Throckmorton, 1976; my dissection). The quadrate protracts rather than retracts during jaw opening and it returns back to its original posterior position when the jaws are closed or nearly closed. During the latter stage, the two ligaments stretch and hold the condyle of the quadrate on both sides. The tension of the two ligaments is able to counteract the continuing posterodorsal pull of the adductors' contribution on the mandible to prevent the quadrate from further posterior movement and thus the jaw articulations are relatively stabilized. Under such a circumstance, the precise tooth occlusion would not be seriously affected at the end of bite in spite of the presence of a mobile quadrate in the agamid lizard.

In contrast, the resultant force of all the adductors acts anterodorsally in the primitive sphenodontidans, as in the living Sphenodon, based on the similar relationship between the centre of origin and the centre of insertion (see above) and alters its direction of action relative to the mandible during the jaw cycle. The resultant force would pull the mandible backward and upward when the jaws are open and pull it forward and upward when the jaws are closed or nearly closed (Fig. 78). If the posterior movement of the quadrate were constricted only by ligaments as in extant lizards, a mobile quadrate, if present, would be effected by the anterodorsal pull of the resultant force when the jaws were nearly closed, i.e. the quadrate would move forward and disrupt the precise shearing bite. In order to avoid this problem, the quadrate in the early sphenodontidans with an incomplete lower temporal bar is firmly fixed to the rest of the skull by the extensive contact between it and the pterygoid and the overlap of the squamosal on its lateral side.

Whiteside (1986) pointed out that the posterodorsal pull of the resultant force of the adductor jaw muscles in sphenodontidans would produce a torque in the quadrate. This torque would cause a posterior twisting of the lateral condyle of the quadrate that is firmly supported by the pterygoid medially but only loosely fixed laterally by the squamosal. Such a twisting would result in disruption of the precise tooth occlusion. From this hypothesis, Whiteside argued that the regrowth of the lower temporal bar was necessary for the

Fig. 78. Changes in the acting direction of the resultant force of all the adductors relative to the mandible during jaw opening in Gephyrosaurus (after Evans, 1980). Thick lines represent the resultant force of all the muscles.



precise shearing bite in the Sphenodontida. As Fraser (1988) mentioned, a partially formed lower temporal bar could provide a point for the attachment of ligaments. If the ligament were present in early sphenodontidans (in which the lower temporal bar is not complete) as is the case in extant lizards, the posterior movement of the lateral side of the quadrate condyle would be restricted when the jaws are open. The direction of the action of the resultant force alters from posterodorsally to anterodorsally during the jaw cycle, the torque developed in the quadrate would result in anterior twisting of the lateral side of the quadrate condyle when the jaws are nearly closed because of the loose attachment. It is therefore suggested that a complete lower temporal bar in later sphenodontidans may have served as a brace to support the lateral side of the quadrate condyle and thus prevent anterior twisting when the jaws are closed. If this were the case, the reduction of the lower temporal bar may have been a primitive feature of the Sphenodontida and a common character shared by the Sphenodontida and the Squamata. On the other hand, the ancestor of the Sphenodontida almost certainly retained a fixed quadrate. From this it is assumed that the latest common ancestor of the Squamata and the Sphenodontida had an incomplete lower temporal bar but a fixed quadrate.

INTERRELATIONSHIPS WITHIN THE SPHENODONTIDA

The advent of phylogenetic systematics has reformed systematic procedures and prompted a re-evaluation of the 'diagnostic features' employed to portray taxonomic assemblages. In contrast with the use of general similarities in more traditional systematic approaches, cladistical methodology puts the emphasis on specialized or derived similarities or characters that are uniquely shared by two or more taxa or groups in defining relationships within monophyletic assemblages. The polarity of a certain character or character state is determined by out-group comparison. An outgroup is the closest relative of the group in question. It can be a species, genus or any taxa in higher taxonomic level. The resulting group relationships are directly obtained from character distribution patterns arranged by the principle of parsimony. In establishing interrelationships within the Sphenodontida I follow the procedures of cladistical methodology (Hennig, 1966; Eldredge and Cracraft, 1980; Wiley, 1981).

Recently, several authors have applied cladistic techniques to the Sphenodontida (Whiteside, 1986; Fraser, 1988; Evans, 1988; Gauthier et al., 1988; Fraser and Benton, 1989). There are a number of points of controversy in the phylogenetic relationships of Homoeosaurus, Palaeopleurosaurus and Clevosaurus. With new information from the genera from China and Homoeosaurus maximiliani, it is necessary to reevaluate the phylogenetic patterns of sphenodontidans.

It is well established that the closest relatives of the Sphenodontida are members of the order Squamata, including lizards, snakes and amphisbeanians. As in the analyses of Whiteside (1986) and Evans (1988), the Squamata serves here as the out-group comparison in determining the polarity of characters that vary within the Sphenodontida.

In my analysis of sphenodontidan relationships, only skull characters are considered because few genera have a well preserved postcranial skeleton and for many nothing is preserved at all. Thirty-six cranial characters have been used for this analysis (Tables 4 and 5). These characters have been selected primarily on the basis of the data set used in Fraser and Benton's analysis (1989). In their data set there are 24 cranial characters. Four have been modified and two have been omitted in my analysis. (6) Frontals and parietals: separate (0), fused (1). This must be divided into two separate characters since the frontals are fused but the parietals are separate in Diphydontosaurus. The reverse condition occurs in Palaeopleurosaurus. (15) Flanges or ridges on palatal tooth row: absent (0), posterolateral ridges or flanges present on some palatine teeth (1). This character can be determined in Sphenodon and in a few fossil genera, but it cannot be satisfactorily appraised in most of the other genera. Therefore, it has been not considered here. (17) Antorbital region: elongate (0), shortened (1). This character has been defined here as antorbital region/skull length (from the tip

Table 4. Cranial characters used for cladistic analysis. Primitive states are indicated by 0, derived states by 1. The character numbers in parentheses after these numbers are from Fraser and Benton (1989).

---

1 Maxilla: contributes to external naris (0), separate by the posterodorsal process of the premaxilla from the external naris (1).

2 Premaxillary process of maxilla: elongate (0), very weak or reduced (1).

3 (5). Lacrimal: present (0), absent (1).

4 (6 partial). Frontals: separate (0), fused (1).

5 (6 partial). parietals: separate (0), fused (1).

6 (19 modified). Parietal width between supratemporal passages: broader than the interorbital width (0), narrower (1).

7 (20). Parietal crest: absent (0), present (1).

8 Supratemporal: present (0), absent (1) (after Gauthier et al., 1988).

9 Parietal foramen: posterior to the line between the anterior margins of the supratemporal fenestrae (0), reaches or crosses the line (1) (modified from Gauthier et al., 1988).

10 (17 modified). Antorbital region/skull length: more than one-fourth (0), less than one-fourth (1).

11 Antorbital region/skull length: more than one-third (0), less than one-third (1).

12 (18 modified). Supratemporal fenestra/orbit: less than three-fourths (0), more than three-fourths (1).

13 (2). Posterior process of dentary: short (0), elongate (1).

14 Coronoid process of dentary: absent or weak (0), pronounced (1).

15 (3). Lower temporal bar: aligned exactly with the maxillary tooth row (0), bows away laterally beyond the limit of the adductor chamber (1).

16 Lower temporal bar: incomplete (0), secondarily complete (1).

17 (25). Retroarticular process: pronounced (0), reduced (1).

18 (26). Quadratojugal-quadrate conch: pronounced (0), reduced (1).

19 (7). Dentition: pleurodont (0), a degree of acrodont (1).

continued

20 (8). Premaxillary teeth: more than 7 acrodont teeth (0), seven or fewer (1).
21 (13). Premaxillary tooth: more than four (0), four or fewer (1).
22 (14). Premaxillary tooth: more than three (0), three or fewer (1).
23 (9). Premaxillae: individual teeth remain discrete in adults (0), premaxillae develop into chisel-like structure in mature individuals (1).
24 (10). Posterior maxillary teeth: simple conical structure (0), presence of a posteromedial ridge or flange (1).
25 (11). Lateral and medial wear facets on marginal teeth: absent or poorly developed (0), well established on both maxillary and mandibular teeth (1).
26 (12). Ridges or flanges on dentary teeth: absent (0), anterolabial ridges or flanges on at least one dentary tooth (1).
27 (28). Extensive posterolingual flanges on some maxillary teeth (at least as long again as the main tooth cone): absent (0), present (1).
28 (1). Lateral palatine tooth row: small (0), enlarged (1).
29 (16). Palatine tooth row: more than one tooth row (0), a single large lateral tooth row (1).
30 Pterygoid teeth: more than two tooth rows (0), two tooth rows or absent (1) (modified from Evans, 1988).
31 Palatine: tapered posteriorly (0), becomes relatively wide posteriorly (1).
32 Central region of pterygoid between three rami: short (0), elongate (1).
33 Parabasisphenoid depression: absent (0), present (1).
34 Pterygoid: enters into the suborbital fenestra (0), precluded from the suborbital fenestra (1).
35 Suborbital fenestra: enclosed by more than two bones (0), only by the palatine and the ectopterygoid (1).
36 (24). Jaw movement: precision-shear bite (0), propalinal (1).

Table 5. Character state data on 14 sphenodontidan genera and Squamata, the designated outgroup. Characters are listed in Table 4. Abbreviations: 0, promotive state; 1, derived state; ?, not known; N, not applicable

		5	10	15	20	25	30	35	
1.	Squ.	00000	00000	00000	00000	00000	00000	00000	0
2.	Gep.	00011	00100	00101	00000	00000	00100	00000	0
3.	Dip.	00110	00100	10111	00011	00000	00100	00000	0
4.	Pla.	00111	00100	00111	10011	10010	10100	00000	0
5.	Pol.	??100	00?01	10111	1??11	11111	??111	0?01?	0
6.	Hom.	00100	00110	00111	11?11	11111	11111	10010	0
7.	Bra.	01100	00?01	11111	10?11	11111	??111	000??	0
8.	Cle.	11100	10000	11111	10011	11111	11111	00011	0
9.	Dia.	??10?	1000?	?1111	?001?	???11	11111	00111	0
10.	Asi.	1110?	00000	11111	?001?	???11	11111	01111	0
11.	Rar.	1110?	00001	11111	?0011	11111	11111	10011	0
12.	Kal.	0?100	11110	01111	10?11	11111	1111?	10010	0
13.	Pal.	00101	11100	01110	00011	11111	11111	01000	0
14.	Sph.	00100	11110	11111	11111	11111	10111	11010	1
15.	Sap.	00?00	11?10	11111	10?NN	NN1NN	N?NNN	100??	?

1, Squamata
2, *Gephyrosaurus*
3, *Diphydontosaurus*
4, *Planocephalosaurus*
5, *Polysphenodon*
6, *Homoeosaurus*
7, *Brachyrhinodon*
8, *Clevosaurus*
9, *Dianosaurus*
10, *Asiacephalosaurus*
11, *Rarojugalosaurus*
12, *Kallimodon*
13, *Palaeopleurosaurus*
14, *Sphenodon*
15, *Sapheosaurus*

of snout to the line between the posterior edges of the squamosals). It can be also divided into two separate characters. One is that antorbital region/skull length (Table 6): more than one-fourth (0), less than one-fourth (1) and the other is that antorbital region/skull length: more than one-third (0), less than one-third (1). (18) Temporal region: short (0), elongate (1). As with (17), this character can be further specified. It has been modified to supratemporal fenestra/orbit: less than three-fourths (0), more than three-fourths (1). This is a particularly useful measure because the supratemporal fenestra and the orbit are preserved in most of known genera and they can be restored with more confidence than other portions of skull. (19) Parietal table: broader than interorbital width (0), narrower (1). The parietal table is the flat area between the two supratemporal fenestrae. It can be confused with the parietal width between the two supratemporal passages when the medial shelf (derived from the lateral side of the parietal table) of the fenestrae is very narrow or not well preserved. For example, in Diphydontosaurus and Brachyrhinodon, the parietal table is not as broad as the interorbital region, but it was often coded conversely in previous analyses by neglecting the presence of the narrow medial shelf of the supratemporal fenestrae. According to the preservation of the parietal region in known genera, it is better to use the parietal width between the supratemporal passages/the interorbital breadth as a cranial character. (27) Breadth of marginal teeth: approximately equal to the length

Table 6. Main ratios of skull in fourteen sphenodontidans

		Length ATO/Skull*	Length STF/Orbit
1	Gephyrosaurus	0.342	0.63
2	Diphydontosaurus	0.304	0.57
3	Planocephalosaurus	0.344	0.52
4	Palaeopleurosaurus	0.343	1.35
5	Brachyrhinodon	0.225	0.93
6	Polysphenodon		0.58
7	Clevosaurus	0.303	1.00
8	Asiacephalosaurus	0.306	0.80
9	Dianosaurus		1.05
10	Rarojugalosaurus	0.233	1.19
11	Homoeosaurus**	0.368	0.45
12	Kallimodon	0.334	0.98
13	Sapheosaurus	0.270	1.09
14	Sphenodon	0.283	0.83

ATO--The antorbital region. STF--The supratemporal fenestra. *--Skull length is from the tip of the snout to the line between the posterior margins of the squamosals. **--Data are based on Homoeosaurus maximiliani (C.M.6438). Source references--1, from Evans, 1980; 2, from Whiteside, 1986; 3 and 7, from Fraser, 1982 and 1988; 4, from Carroll, 1985; 5 and 6, from Fraser and Benton, 1989; 11, 12 and 13, from Cocude-Michel, 1963.

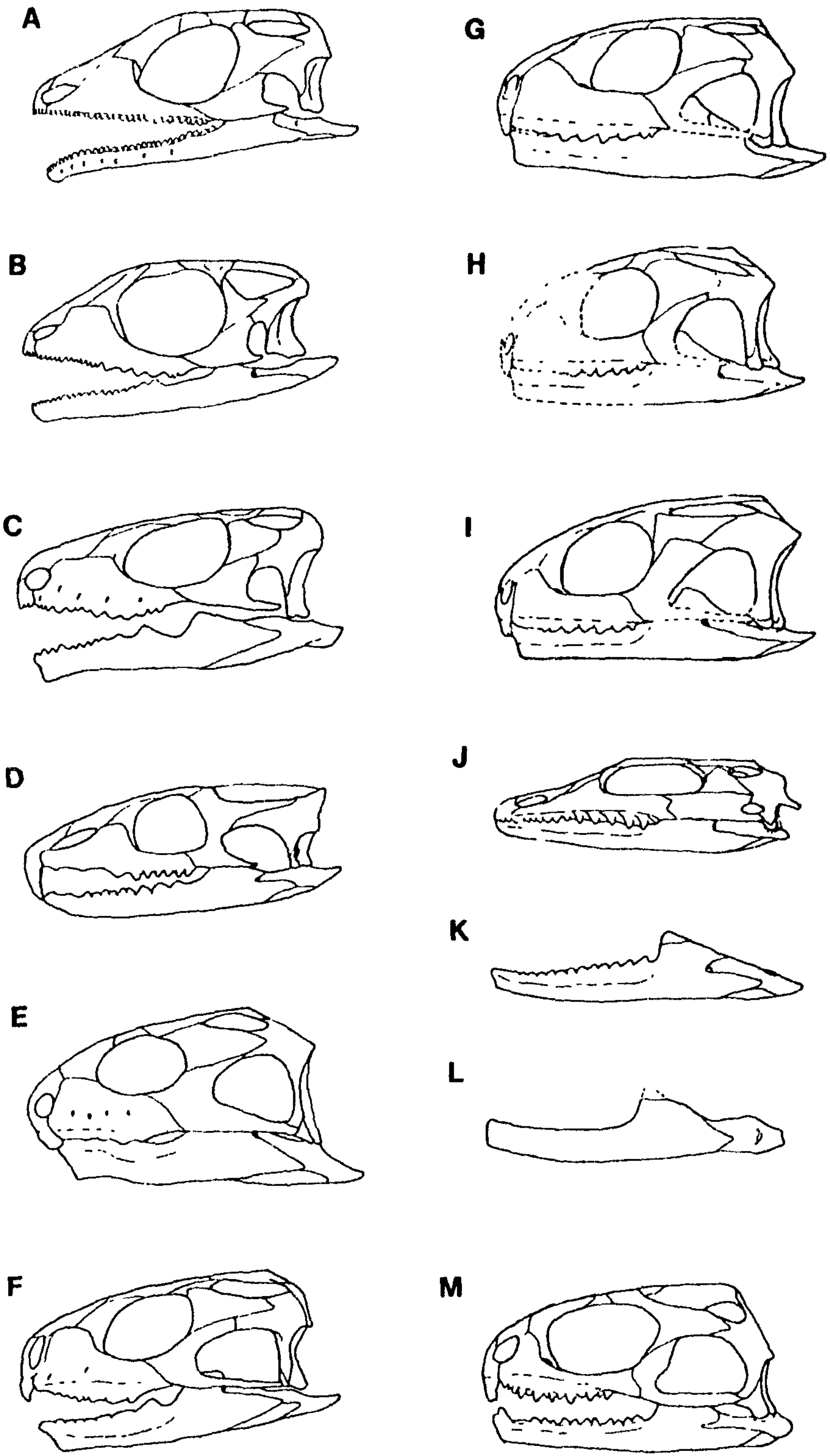
(0), greatly expanded mediolaterally (1). Among all known sphenodontidans only Eilenodon and Toxolophosaurus show a derived condition of the character. These two genera will not be involved in my analysis because the remains of the skull are not preserved. This character is hence omitted.

Among the remaining characters, Nos. 14, 9, and 8 are derived from those used by Gauthier et al (1988) and character 30 is modified from that used in Evans' analysis (1988). The characters that are newly added to this analysis are as follows:

Character 1--Maxilla contributes to the margin of the external naris (0), separated from the external naris (1). In most sphenodontidans the maxilla forms the ventral or posteroventral margin of the external naris (Fig. 79) as in other lepidosauromorphs. The separation of the maxilla from the external naris is a synapomorphy of the Archosauromorpha (Benton, 1984; Gauthier, 1984; and Carroll, 1988a). The exclusion of the maxilla from the external naris has been independently evolved in certain sphenodontidans and is considered here as a derived state within the Sphenodontida.

Character 2--Premaxillary process of maxilla is very pronounced and forms the ventral margin of the external naris (0), very weak or reduced and only contributes to the posteroventral margin of, or precluded from, the external naris (1). In common with squamates and other lepidosauromorphs, most sphenodontidans show a maxilla in which the premaxillary process is elongate and extends

Figure 79. Lateral views of the skulls and mandibles of A, Gephyrosaurus; B, Diphydontosaurus; C, Planocephalosaurus; D, Palaeopleurosaurus; E, Brachyrhinodon; F, Clevosaurus; G, Asiacephalosaurus; H, Dianosaurus; I, Rarojugalosaurus; J, Homoeosaurus; K, Kallimodon; L, Sapheosaurus; and M, Sphenodon. (A, after Evans, 1880; B, after Whiteside, 1986; C, after Fraser, 1982; D, after Carroll, 1985; E, after Fraser and Benton, 1989; F, after fraser, 1988; K and L, after Cocude-Michel, 1963).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forwards along the ventral edge of the external naris. The reduction of the premaxillary process of the maxilla only occurs in some genera of the Sphenodontida; it is certainly a derived pattern in the group.

Character 16--Lower temporal bar is incomplete (0), complete (1). A complete lower temporal bar has a long history in the Diapsida. It is certainly a primitive character state. However, in common with all squamates and some primitive diapsid groups, certain early sphenodontidans show that the lower temporal bar was incomplete posteriorly. As argued above, in the common ancestry of the Squamata and the Sphenodontida the lower temporal bar may have been incomplete and a complete lower temporal bar in late sphenodontidans could be secondarily evolved. The different sutural patterns of the lower temporal bar demonstrate that the completeness of the bar is not homologous between the late sphenodontidans and other diapsids. Evidence from the ontogeny of the living <u>Sphenodon</u> also supports this argument (Whiteside, 1986). Consequently, the complete lower temporal bar is considered derived within the Sphenodontida.

Character 31--Palatine is tapered posteriorly (0), relatively broad (1). A posteriorly tapered palatine occurs in early lepidosauromorphs and squamates. Similarly, most early sphenodontidans have a palatine that tapers gradually posteriorly. However, the great width of the posterior part of the bone in the oldest known diapsid <u>Petrolacosaurus</u> (Reisz, 1981) indicates that character 31 may have had a similar evolutionary history to that of character 16. The broadened posterior part of the palatine in late sphenodontidans is a secondary requisition that is probably associated with selective pressure for the development of a propalinal jaw movement. Although some squamates (e.g. the iguanian Sceloporus, Larsen and Tanner,1974) possess a palatine that is not tapered posteriorly, this condition cannot be homologous with that seen in the late sphenodontidans.

Character 32--The central region of the pterygoid between the three rami is short (0), elongate (1). In most sphenodontidans the central region of the pterygoid is very short, as in the early lepidosauromorph Youngina (Gow, 1975; Carroll, 1988). This is a common feature in lizards and other lepidosauromorphs. Some lizards such as Elgaria (Rieppel, 1980) display an elongate central region of the pterygoid. This pattern cannot be homologous with that seen in sphenodontidans since these animals belong to two distinct groups that are differentiated by many synapomorphies. The elongation of the central region of the pterygoid is believed to be a derived condition within the Sphenodontida.

Character 33--Parabasisphenoid depression is absent (0), present (1). The parabasisphenoid forms the anterior floor of the braincase. It is usually concave ventrally from side to side in both squamates and sphenodontidans. The occurrence of a depression on the posteroventral surface of the parabasisphenoid is apparently a derived state in the group.

Character 34--Pterygoid forms the posteromedial margin of the suborbital fenestra (0), precluded from the suborbital fenestra (1). In the oldest known diapsid Petrolacosaurus the pterygoid does not enter the suborbital fenestra. It seems that the polarity of the character has been wrongly coded here. However, in common with archosauromorphs, the palatine and the ectopterygoid of lepidosauromorphs lose contact at the posteromedial corner of the suborbital fenestra, thereby the pterygoid contributes to the margin of the fenestra. As with characters 16 and 31, the separation of the pterygoid from the suborbital fenestra within the Sphenodontida (Fig. 80) should be considered as secondarily derived within the group.

Character 35--Suborbital fenestra is enclosed by more than two bones (0), only by the palatine and the ectopterygoid (1). Lizards and other lepidosauromorphs have a suborbital fenestra that is enclosed by the palatine, maxilla, ectopterygoid and pterygoid. This pattern was not changed in many early sphenodontidans. Character 34 has already stated that in some sphenodontidans the pterygoid had been separated by the contact of the palatine with the ectopterygoid from the posteromedial margin of the fenestra, showing a derived condition. Furthermore, in some other genera the maxilla is excluded from the lateral margin of the fenestra by the connection of the ectopterygoid with the maxillary process of the palatine (Fig. 81). The suborbital fenestra is exclusively surrounded by these two bones. Therefore, this condition shows a more derived pattern within the Sphenodontida.

More than twenty sphenodontidan genera have been

Figure 80. Ventral views of the skulls of

A, *Gephyrosaurus*; B, *Diphydontosaurus*;

C, *Planocephalosaurus*; D, *Palaeopleurosaurus*;

E, *Brachyrhinodon*; F, *Polysphenodon*;

G, *Clevosaurus*; H, *Asiacephalosaurus*;

I, *Dianosaurus*; J, *Rarojugalosaurus*;

K, *Homoeosaurus*, L, *Kallimodon*; M, *Sapheosaurus*;

and N, *Sphenodon*. (A, after Evans, 1980;

B, after Whiteside, 1986; C, after Fraser,

1982; D, after Carroll, 1985; E and F, after

Fraser and Benton, 1989; G, after Fraser, 1988;

L and M, after Cocude-Michel, 1963).

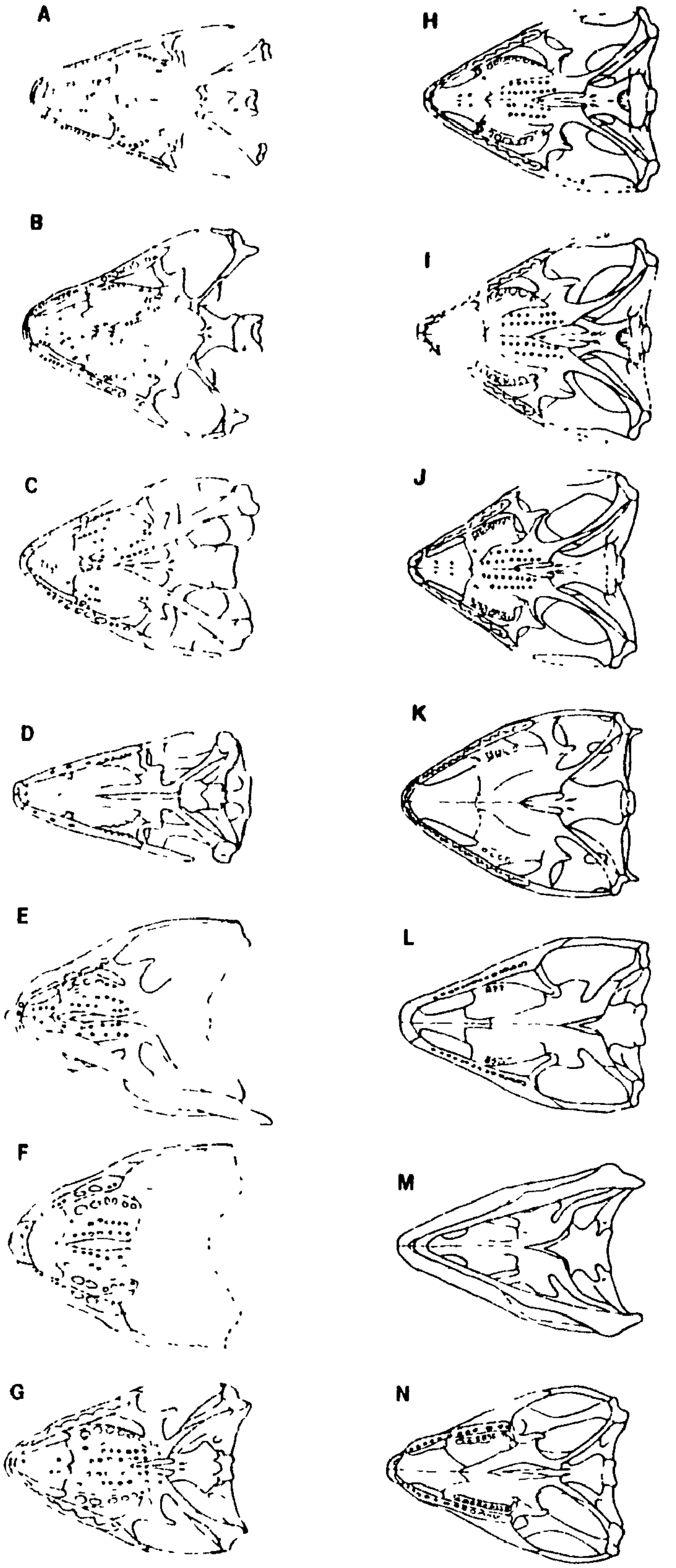
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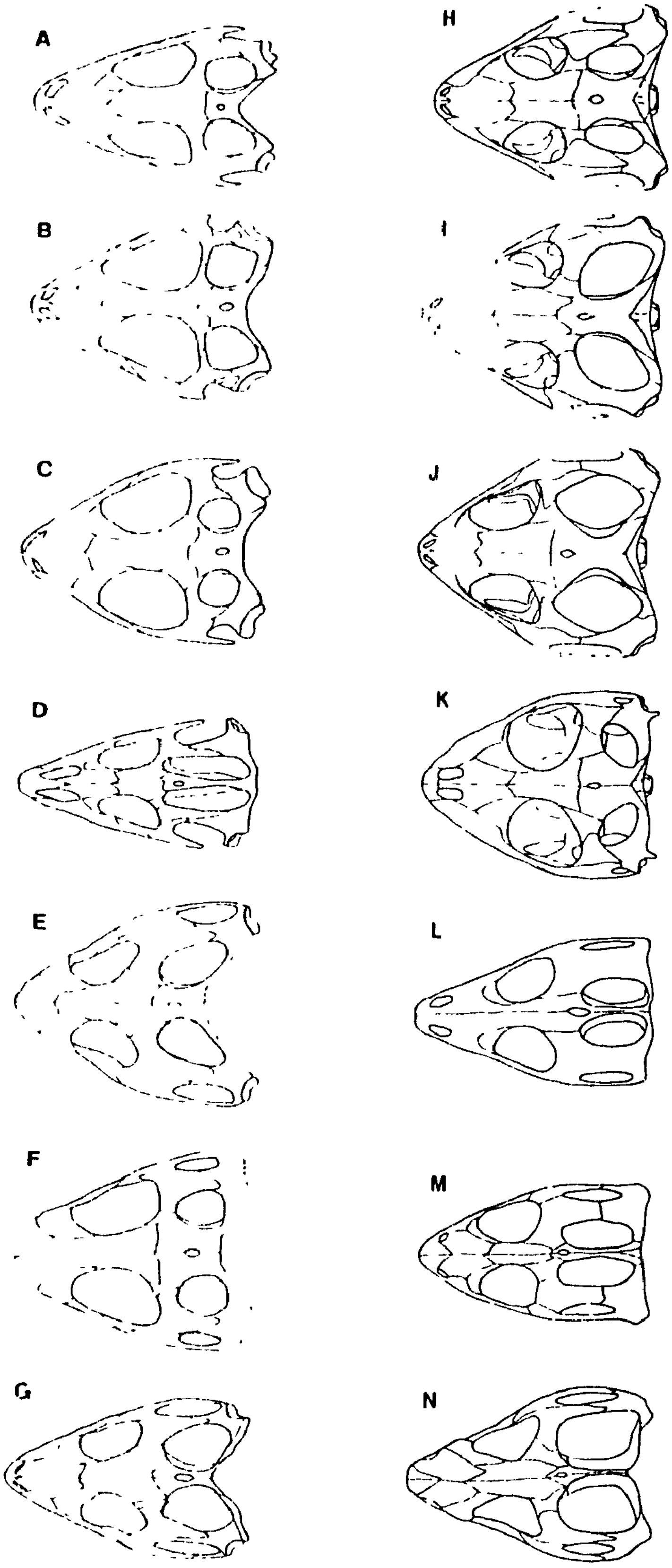
Figure 81. Dorsal views of the skulls of A, *Gephyrosaurus*; B, *Diphydontosaurus*; C, *Planocephalosaurus*; D, *Palaeopleurosaurus*; E, *Brachyrhinodon*; F, *Polysphenodon*; G, *Clevosaurus*; H, *Asiacephalosaurus*; I, *Dianosaurus*; J, *Rarojugalosaurus*; K, *Homoeosaurus*; L, *Kallimodon*; M, *Sapheosaurus*; and N, *Sphenodon*. (A, after Evans, 1980; B, after Whiteside, 1986; C, after Fraser, 1982; D, after Carroll, 1985; E and F, after Fraser and Benton, 1989; G, after Fraser, 1988; L and M, after Cocude-Michel, 1963).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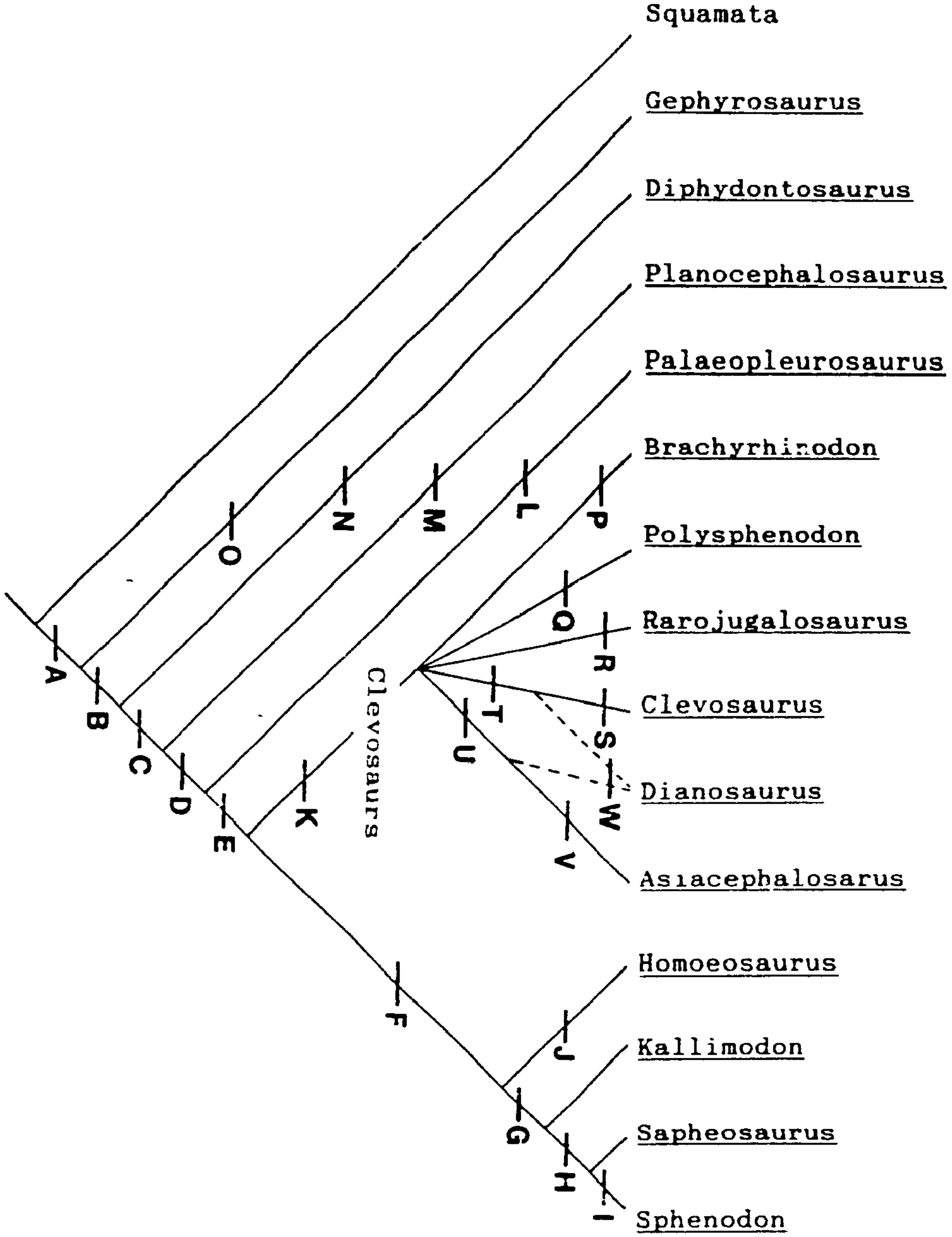
described. Owing to incompleteness, only fourteen of them with more than 52% of the total character set have been considered in my analysis (Table 5). The analysis is carried out using Mix Parsimonious Algorithm in the PHYLIP Package (Version 3.1 written by J. Felsentein). The trees were rooted by applying the A (ancestral states) option, and the J (Jumble with 249 as Random Number Seed) and the Global Rearrangement options were invoked. This program generated 9 equally parsimonious cladograms that are all congruent in a broad sequence of sister-group relationship from the Squamata, through Gephyrosaurus, Diphydontosaurus, Planocephalosaurus, Palaeopleurosaurus, the subgroup clevosaurs (Gauthier et al., 1988, but see below), Homoeosaurus, Kallimodon, Sapheosaurus to the living Sphenodon (Fig. 82). These cladograms resemble results of most recent cladistic analyses in that Gephyrosaurus, Diphydontosaurus and Planocephalosaurus form successively closer sister-groups of the other sphenodontidan genera and subgroups (Whiteside, 1986; Evans, 1988; Fraser and Benton, 1989). The primary contradictions between this and previous analyses concern the relationships of Homoeosaurus and Palaeopleurosaurus to the other genera or subgroups.

It has been established that a broad parietal width between the two supratemporal passages and a flat parietal table (characters 6 and 7) are plesiomorphic conditions in the Sphenodontida. In common with most early genera, the parietal width is greater than the interorbital breadth and the parietal table is not crested in Homoeosaurus. Recent

Figure 82. A consensus cladogram based on the original 9 equally parsimonious cladograms yielded by Mix Parsimonious Algorithm in the PHYLIP Package Version 3.1 (index: 0.643), depicting group relationships of the Sphenodontida.

A-Characters 4.8.13.15.28
B-Characters 3.14.19.20
C-Characters 21.24.26
D-Characters 12.22.23.25.27.29.30
E-Characters 16.34
F-Characters 9.31
G-Characters 6.7
H-Character 11
I-Characters 17.18.32.36
J-Character 17
K-Characters 2.11
L-Characters 5.6.7.32
M-Characters 5.16
N-Character 11
O-Character 5
P-Character 10
Q-Character 10
R-Characters 1.10.35
S-Characters 1.35
T-Character 6
U-Character 33
V-Characters 6.32.35
W-Character 35

The underlined characters are reversed at least once in the cladogram. The homoplastic characters can be read from each note (see text for more details).


Squamata
Gephyrosaurus
Diphydontosaurus
Planocephalosaurus
Palaeopleurosaurus
Brachyrhinodon
Polysphenodon
Rarojugalosaurus
Clevosaurus
Dianosaurus
Asiacephalosarus
Homoeosaurus
Kallimodon
Sapheosaurus
Sphenodon
Clevosaurs
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cladistic analyses have shown that a relatively short temporal region (character 12) is another primitive character in the group. Homoeosaurus possesses a temporal region that is relatively the shortest among the known sphenodontidans. With a broad parietal width, a flat parietal table and a short temporal region, Homoeosaurus has been considered to be more primitive than Palaeopleurosaurus (Evans, 1988; Fraser, 1986; Fraser and Benton, 1989).

Contrary to previous cladistic arrangements, the present data indicate that Homoeosaurus is more derived than Palaeopleurosaurus. Character 9 (the parietal foramen reaching or crossing the line between the anterior margins of the supratemporal fenestrae) and character 31 (the relatively widened posterior part of the palatine) link Homoeosaurus with Kallimodon, Sapheosaurus and Sphenodon as a monophyletic subgroup. Furthermore, these four genera are united with the clevosaurs as a monophyletic subgroup at a higher level by sharing character 16 (a complete lower temporal bar) and character 34 (the exclusion of the pterygoid from the suborbital fenestra), although these two characters are not entirely clear in some genera. In Palaeopleurosaurus, the lower temporal bar has a break posteriorly and the pterygoid forms the posteromedial margin of the suborbital fenestra. In these aspects, Palaeopleurosaurus resembles the more primitive genera, Planocephalosaurus (in this genus some specimens show a complete lower temporal bar), Diphydontosaurus and Gephyrosaurus.

As shown in figure 82, relationships among Homoeosaurus, Kallimodon, Sapheosaurus and Sphenodon have been also established in the present analysis. The last three genera form a monophyletic subgroup. They share two characters: character 6 (the narrow parietal width) and character 7 (the crested parietal table). These characters are considered to have evolved convergently in Palaeopleurosaurus. Character 11 (antorbital region/skull length is less than one-third) links Sapheosaurus and Sphenodon as a less inclusive subgroup within the Sphenodontida. However, by convergence, the clevosaurs also possesses this character.

The possession of characters 12, 22, 23, 25, 27, 29 and 30 shows that Clevosaurus is more derived than Gephyrosaurus, Diphydontosaurus and Planocephalosaurus. According to Fraser and Benton (1989), Clevosaurus is even more derived than Brachyrhinodon and Polysphenodon in having a parietal table that is narrower than the interorbital width. However, the relationships of Clevosaurus with the other derived sphenodontidans could not be clarified in their analysis. According to the present analysis, Clevosaurus has been grouped with Brachyrhinodon, Polysphenodon, Dianosaurus, Asiacephalosaurus, and Rarojugalosaurus as a monophyletic subgroup that can be defined by a very weak or reduced premaxillary process of the maxilla (character 2) and a relatively short antorbital region (character 11), although these characters are unknown in Dianosaurus. This subgroup has been informally referred to here as the clevosaurs for reason of convenience. This usage contrasts with that in Gauthier et al (1988) in which only Clevosaurus and Planocephalosaurus included. However, most recent cladistic analyses have questioned such a close relationship between these two genera and demonstrated that Planocephalosaurus is more primitive than Clevosaurus (Whiteside, 1986; Evans, 1988; Fraser and Benton 1989). Unfortunately, the present character set offered little solution of interrelationships within the clevosaurs.

CONCLUSIONS

So far as is known, all the Late Triassic-Early Jurassic genera of the Sphenodontida possessed a lizard-like tympanic frame. Evidence from braincase indicates that the fenestra rotundum, which has long been considered a unique compensatory structure for the movement of inner ear fluid in the ear of lizards (Gauthier et al., 1988) was probably also common to these early sphenodontidans. The middle ear apparatus of these early forms was very similar to that of lizards in both configuration and function and a lizard-style impedance matching middle ear was presumably established in the ancestor of the Lepidosauria. The alteration of the tympanic frame from ventral to dorsal support in Homoeosaurus maximiliani demonstrates that a functional tympanum was retained in certain Late Jurassic-Early Cretaceous sphenodontidans, rather than lost as early as Triassic times (Robinson, 1973). It is apparent that so-called "primitive" aspects of the middle ear apparatus of the living Sphenodon must have evolved within the group, perhaps in relationship to tongue feeding and a burrowing life.

Functional analysis of the adductor jaw musculature shows that the streptostylic quadrate of the Squamata is derived in the Lepidosauria and a complete lower temporal bar of later sphenodontidans is re-evolved within the group. The latest common ancestor of the Squamata and Sphenodontida had a skull with an incomplete lower temporal bar but a fixed quadrate.

From the current study, the living Sphenodon cannot be considered a "living fossil", representative of early diapsid reptiles, as previously supposed but a specialized lepidosaur. On the contrary, lizards should be thought of as more primitive in having an impedance matching middle ear and an incomplete lower temporal bar that have changed little since they were first established in the ancestors of lepidosaurs.

The limited knowledge of the anatomy of many genera is shown to be responsible for continuing uncertainties concerning the interrelationships within the Sphenodontida (Evans, 1984; Carroll, 1985; Fraser, 1986; Whiteside, 1986; Gauthier et al., 1988; Fraser and Benton, 1989). More than one-third of the 25 known sphenodontidans are omitted in most phylogenetic analyses because of poor preservation. The specific relationship among and between sphenodontidans will only be resolved by the discovery of additional material.

REFERENCES

Baird, I. L. (1970): The anatomy of the repilian ear. In Biologyof the Reptilia (eds. C. Gans and T. S. Parsons), **2**:193-275. London & New York: Academic Press.

Barghusen, H. R. (1972): The origin of the mammalian jaw apparatus. In Morphology of the Maxillomandibular Apparatus (ed. G. H. Schumacher):26-32. Leipzig: VEB Georg Thieme.

Benton, M. J. (1983): The Triassic reptile Hyperodapedon from Elgin: functional morphology and relationships. Phil. Trans. Roy. Soc. Lond., **302**:605-720.

Benton, M. J. (1984): The relationships and early evolution of the Diapsida. In The Structure, Development and Evolution of Reptiles (ed. M. W. J. Ferguson). Linnaean Soc. London, Symp. Ser., **52**:573-596. Cambridge University Press and Academic Press.

Benton, M. J. (1985): Classification and phylogeny of the diapsid reptiles. Zool. J. Linn. Soc., **84** (2):97-164.

Bien, M. N. (1941): "Red Beds" of Yunnan. Geol. Soc. China, **21**:159-168.

Bramble, D. M. (1978): Origin of the mammalian feeding complex; models and mechanisms. Paleobiology, **4**:271-301.

Brinkman, D. (1981): The origin of the crocodiloid tarsi and the interrelationships of thecodontian reptiles. Breviora, **464**:1-23.

Carroll, R. L. (1976): The oldest known rhynchosaur. Ann. S. Afr. Mus., **72**:37-57.

Carroll, R. L. (1977): The origin of lizards. In Problems in Vertebrate Evolution (eds. S. M. Andrew, R. S. Miles & A. D. Walker). Linnaean Society Symposia Series **4**:359-396.

Carroll, R. L. (1985): A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Palaeontographica, Abt., A, **189**:1-28.

Carroll, R. L. (1988a): Vertebrate Paleontology and Evolution. New York: W. H. Freeman and Company, 698 pp.

Carroll, R. L. (1988b): Late Palaeozoic and Early Mesozoic lepidosauromorphs and their relation to lizard ancestry. In Phylogenetic Relationships of the Lizard Families (eds. R. Estes and G. Pregill):99-118. Stanford, California: Stanford Univ. Press.

Carroll, R. L. & Holmes, R. (1980): The skull and jaw musculature as guides to the ancestry of salamanders. Zool. J. Linn. Soc., **68**:1-40.

Chatterjee, S. (1974): A rhynchosaur from the Upper Triassic Maleri Formation of India. Phil. Trans. Roy. Soc., Ser. B, **267**:209-260.

Cocude-Michel, M. (1963): Les rhynchocephales et les sauries des calcaies lithographiques (Jurassique Superieur) d'Europe occidentale. Nouv. Arch. Mus. d'Hist. Nat. Lyon., 7:1-187.

Colbert, E. H. (1966): A gliding reptile from the Triassic of New Jersey. Amer. Mus. Novit., **2230**:1-23.

Colbert, E. H. (1970): The Triassic gliding reptile *Icarosaurus*. Bull. Amer. Mus. Nat. Hist., **143**:89-142.

Cong, L. Y., Hou, L. H. & Wu, X. C. (1984): Age variation in the skull of *Alligator sinensis* Fauvel in topographic anatomy. Acta Herpt. Sinica, **3** (2):1-14.

Cong, L. Y., Hou, L. H. & Wu, X. C. (Submitted): The Gross Anatomy of *Alligator sinensis* Fauvel: Integument, Osteology and Myology. Beijing, China: Science Press, Academia Sinica.

Crompton, A. W. & Parker, P. (1978): Evolution of the mammalian masticatory apparatus. Amer. Sci., **66**:192-201.

Cruickshank, A. R. I. (1972): The proteosuchian thecodonts. *In* Studies in Vertebrate Evolution (eds. K. A. Joysey & T. S. Kemp):89-119. Oliver & Boyd, Edinburgh.

Daugherty, C. H., Cree, A., Hay, J. M. & Thompson, M. B. (1990): Neglected taxonomy and continuing extinctions of tuatara (*Sphenodon*). Nature, **347**:177-179.

Dawbin, W. H. (1982): The tuatara *Sphenodon punctatus* (Reptilia: Rhynchocephalia): a review. *In* New Zealand Herpetology (ed. D.G. Newman):149-182. Wellington: Victoria University.

De Beer, G. R. (1985): The Development of the Vertebrate Skull. The University of Chicago Press, 515 pp.

Edgeworth, F. H. (1931): On the development of the external ocular, masticatory, and hyoid muscles of *Sphenodon*. Proc. Zool. Soc. Lond. B, **101**:803-808.

Edgeworth, F. H. (1935): The Cranial Muscles of Vertebrates. Cambridge: University Press, 493 pp.

Eldredge, N. & Cracraft, J. (1980): Phylogenetic Patterns and the Evolutionary Process. New York: Columbia Univ. Press.

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

Evans, S. E. (1980): The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool. J. Linn. Soc., **70**:203-264.

Evans, S. E. (1981): The postcranial skeleton of the Lower Jurassic eosuchian Gephyrosaurus bridensis. Zool. J. Linn. Soc., **73**:81-116.

Evans, S. E. (1984): The classification of the Lepidosauria. Zool. J. Linn. Soc., **82**:87-100.

Evans, S. E. (1986): The braincase of Prolacerta broomi (Reptilia: Triassic). N.Jb. Geol. Palaont. Abh., **173**(2):181-200.

Evans, S. E. (1987): The braincase of Youngina capensis (Reptilia: Diapsida; Permian). N.Jb. Geol. Palaont. Mh., **1987**(H.4):193-203.

Evans. S. E. (1988): The early history and relationships of the Diapsida. In The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds (ed. M. J. Benton). Systematic Association Special Volume **35A**:221-260. Oxford: Clarendon Press.

Ewer, R. F. (1965): The anatomy of the thecodont reptile Euparkeria capensis Broom. Phil. Trans. Roy. Soc. Lond., Ser. B, **248**:379-435.

Fabre, J. (1981): Les rhynchocephales et les pterosauriens a crete parietale du Kimeridgien superieur - Berriasien d'Europe occidentale. Le gisement de Canjuers (Var-France) et ses abords (Editions de la Fondations Singer), Polignac.

Fraser, N. C. (1982): A new rhynchocephalian from the British Upper Trias. Palaeontology, **25**:709-725.

Fraser, N. C. (1985): Vertebrate fauna from Mesozoic fissure deposits of South West Britain. Mod. Geol. **9**:273-300.

Fraser, N. C. (1986): New Triassic sphenodontids from South-west England and a review of their classification. Palaeontology, **29**:165-186.

Fraser, N. C. (1988): The osteology and relationships of Clevosaurus (Reptilia: Sphenodontida). Phil. Trans. Roy. Soc. Lond., Ser. B, **321**:125-178.

Fraser N. C. & Benton, M. J. (1989): The Triassic reptiles Brachyrhinodon and Polysphenodon and the relationships of the sphenodontids. Zool. J. Linn. Soc., **96**:413-445.

Fraser, N. C. & Walkden, G.M. (1984): The postcranial skeleton of Planocephalosaurus robinsonae. Palaeontology, **27**:575-595.

Gaffney, E. (1980): Phylogenetic relationships of the major groups of amniotes. In The Terrestrial Environment and the Origin of Land Vertebrates (ed. A. Panchen):593-610. London/New York: Academic Press.

Gans, C. & Wever, E. G. (1976): Ear and hearing in Sphenodon punctatus. Proc. Natl. Acad. Sci. USA., **78** (11):4244-4246.

Gauthier, J. (1984): A Cladistic Analysis of the Higher Systematic Categories of the Diapsida. Ph.D. thesis, Department of Paleontology, University of California, Berkeley. University Microfilms #85-12825, Ann Arbor, Michigan.

Gauthier, J., R. Estes, & K. de Queiroz. (1988): A phylogenetic analysis of Lepidosauromorpha. In Phylogenetic Relationships of the Lizard Families (eds. R. Estes and G. Pregill):15-98. Stanford, California: Stanford Univ. Press.

Goin, C. J., Goin, O. B. & Zug, G. R. (1978): Introduction to Herpetology, 3 rd. ed. New York: W. H. Freeman and Company, 378 pp.

Gorniak, G. C., Rosenberg, H. I & Gars, C. (1982): Mastication in the Tuatara Sphenodon punctatus (Reptilia: Rhynchocephalia) Structure and Activity of the Motor System. J. Morph., **171**:321-353.

Gow, C. E. (1975): The morphology and relationships of Younqina capensis Broom and Prolacerta broomi Parrington. Palaeont. Afr., **18**:89-131.

Gow, C. E. & Raath, M. A. (1977): Fossil vertebrate studies in Rhodesia: sphenodontid remains from the Upper Triassic of Rhodesia. Palaeont. Afr., **20**:121-122.

Gunther, A. (1867): Contribution to the anatomy of Hatteria (Rhynchocephalus, Owen). Phil. Trans. Roy. Soc., Part 2:1-34.

Haas, G. (1973): Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In Biology of the Reptilia (ed. C. Gans), 4:285-483. London & New York: Academic Press.

Hennig, W. (1966): Phylogenetic Systematics. Univ. Ill., Urbana, 263 pp.

Hoffstetter, R. (1955): Rhynchocephalia. Traite de Paleont., 5:556-76.

Hoffstetter, R. (1964): Les Sauria du Jurassique superieur et specialement les Gekkota de Baviere et de Mandchourie. Senckenberg Biol. T, 45:281-324.

Huene, F. von (1910): Uber einen echten Rhynchocephalen aus der Trias von Elgin, Brachyrhinodon taylori. N.Jb. Min. Geol. Pal., 2:29-62.

Huene, F. von. (1946): Die grossen stamme der Tetrapoden im den geologischen Zeiten. Biologischen Zentralblatt. 65 (7/12):266-275.

Hughes, B. (1963): The earliest archosaurian reptiles. S. Afr. J. Sci., 135:3-59.

Huxley, T. H. (1869): On Hyperodapedon. Q. J. Geol. Soc. Lond., 25:138-152.

Kuhn, O. (1969): Handbuch der Palaoherpetologie, part 9: 74 pp., Proganosauria-Protorosauria. Gustav Fischer Verlag, Stuttgart.

Lakjer, T. (1926): Studien uber die Trigeminusversorgte Kaumuskulatur der Sauropsiden:1-154. Copenhagen: C. A. Rietzel.

Larsen, K. R. & Tanner, W. W. (1974): Numeric analysis of the lizard genus Sceloporus with special reference to cranial osteology. Great Basin Nat. **34** (1):1-41.

Liem, K. F. (1977): Musculoskeletal system. In Chordate Structure and Function (ed. A. G. Kluge):179-269. New York: Macmillan.

Luther, A. (1914): Uber die vom N. trigeminus versorgte Muskulatur der Amphibien mit einem vergleichenden Ausblick uber den Adductor mandibulae der Gnathostomen, und einem Beitrag zum Vertandnis der Orrganisation der Anurenlarven. Acta. Soc. Sci. Fenn., **44** (7):1-151.

Murry, P. A. (1987): New reptiles from the Upper Triassic Chinle Formation of Arizona. J. Paleont. **61** (4):773-786.

Newman, D. G. (1982): Tuatara, Sphenodon punctatus, and burrows, Stephens Island. In New Zealand Herpetology (ed. D. G. Newman):213-224. Wellington: Victoria University.

Oelrich, T. M. (1956): The anatomy of the head of Ctenosaura pectinata (Iguanidae). Misc. Publ. Mus. Zoo. Univ. Mich., **94**:1-122.

Olsen, P. E. (1980): A comparison of vertebrate assemblages from the Newark and Hartford Basins (early Mesozoic, Newark Supergroup) of eastern North America. In Aspects of Vertebrate History (ed. L.L. Jacobs):35-53. Flagstaff: Museum of Northern Arizona Press.

Ostrom, J. H. (1962): On the constrictor dorsalis muscle of Sphenodon. Copeia, **1962**:732-735.

Owen, R. (1845): Description of certain fossil crania discovered by A. G. Bain, esq., in the southeast extremity of Africa, referable to different species of an extinct genus of Reptilia (Dicynodon), and indicative of a new tribe or suborder of Sauria. Trans. Geol. Soc. Lond., **7** (2):59-84.

Patterson, C. (1981): Significance of fossils in determining evolutionary relationships. Ann. Rev. Ecol. Syst., **12**:195-223.

Patterson, C. (1982): Morphological characters and homology. In Problems of Phylogenetic Reconstruction (eds. K.A. Joysey & E. Friday):21-74. London: Academic Press.

Poglayen-Neuwall, I. (1953): Untersuchungen Uber die Trigeminusmuskulatur von Hatteria. Z. Wissensch. Zool. **157**:57-76.

Reisz, R. (1981): A diapsid reptile from the Pennsylvanian of Kansas. Spec. Pap. Univ. Kans. Mus. Nat. Hist., **7**:1-74.

Rich, T. H. V., Molnar, R. E. & Rich, P. V. (1983): Fossil vertebrates from the Late Jurassic or Early Cretaceous Kirkwood Formation, Algoa Basin, southern Africa. Trans. Geol. Soc. S. Afr., **86**:281-291.

Rieppel, O. (1978): Streptostyly and muscle function in lizards. Experientia, **34**:776-777.

Rieppel, O. (1979): A cladistic classification of primitive snakes based on skull structure. Z. Zool. Syst. Evolut. forsch., **17**:140-150.

Rieppel, O. (1980): The perilymphatic system of the skull of *Typhlops* and *Acrochordus*, with comments on the origin of snakes. J. Herpet. **14** (1):105-108.

Rieppel, O. & Grorowski, R. W. (1981): The loss of the lower temporal arcade in diapsid reptiles. Zool. J. Linn. Soc., **72** (3):203-217.

Rieppel, O. (1985): The recessus scalae tympani and its bearing on the classification of reptiles. J. Herpet. **19**(3):373-384.

Robinson, P. L. (1962): Gliding lizards from the Upper Keuper of Great Britain. Proc. geol. Soc. Lond., **1061**:137-136.

Robinson, P. L. (1973): A problematic reptile from the British Upper Trias. J. Geol. Soc. Lond., **129** (5):457-479.

Robinson, P. L. (1976): How *Sphenodon* and *Uromastyx* grow their teeth and use them. *In* Morphology and Biology of Reptiles (ed. A. d'A. Bellairs & C. B. Cox):43-64. London: Academic Press.

Romer, A. S. (1956): Osteology of the Reptiles. University of Chicago Press.

Schaeffer, B. & Rosen, D. E. (1961): Major adaptive levels in the evolution of the actinopterygian feeding mechanism. Amer. Zool., **1**:187-204.

Schumacher, G. H. (1973): The head muscles and hyolaryngeal skeleton of turtles and crocodilians. *In* Biology of the Reptilia (ed. C. Gans), **4**:101-194. London & New York: Academic Press.

Simmons, D. J. (1965): The non-therapsid reptiles of the Lufeng Basin, Yunnan, China. Fieldiana:Geol., **15** (1):1-93.

Sinclair, A. G. & Alexander, R. M. (1987): Estimates of forces exerted by the jaw muscles of some reptiles. J. Zool. Lond., **213**:107-115.

Smith, K. (1980): Mechanical significance of streptostyly in lizards. Nature, **283**:778-779.

Smith, K. (1982): An electromyographic study of the function of the jaw adducting muscles in Varanus exanthematicus (Varanidae). J. Morph. **173**:137-158.

Sun, A., G. Cui, Y. Li, and X. Wu (1985): A verified list of Lufeng Saurischian Fauna. Vert. PalAsia. **22**:1-12.

Throckmorton, G. S. (1976): Oral food processing in two herbivorous lizards, Iguana iguana and Uromastix aegyptius. J. Morph. **148**:363-390.

Throckmorton, G. S. (1978): Action of the pterygoideus muscle during feeding in lizard Uromastix aegyptius. Anat. Rec. **190**:217-222.

Throckmorton, G. S. (1980): The chewing cycle in the herbivorous lizard Uromastix aegyptius (Agamidae). Arch. Oral. Biol. **25**:225-233.

Throckmorton, G. S., J. A. Hopson, & Parks, P. (1981): A redescription of Toxolophosaurus cloudi Olson, a Lower Cretaceous herbivorous sphenodontid reptile. J. Paleont. **55**:586-597.

Thulborn, R. A. (1980): The ankle joint of archosaurs. Alcheringa, **4**:241-261.

Toerien, M. J. (1962): The sound-conducting systems of lizards without tympanic membranes. Evolution, **17**:540-547.

Tumarkin, A. (1955): On the evolution of the auditory conducting apparatus: A new theory based on functional considerations. Evolution, Lancaster, **9**:221-243.

Walker, A. D. (1961): Triassic reptiles from the Elgin area: Stagonolepis, Dasygnathus and their allies. Phil. Trans. Roy. Soc. Lond. Ser. B, **244**:103-204.

Walker, A. D. (1972): New light on the origin of birds and crocodiles. Nature, **237**:257-263.

Walls, G. Y. (1982): Provisional results from a study of the feeding ecology of the tuatara (Sphenodon punctatus) on Stephens Island. In New Zealand Herpetology (ed. D. G. Newman):271-276. Wellington: Victoria University.

Wever, E. G. (1978): The Reptile Ear. Princeton, New Jersey: Princeton University Press, 1024 pp.

Whiteside, D. I. (1986): The head skeleton of the Rhaetian sphenodontid Diphydontosaurus avonis gen. et sp. nov. and the modernizing of a living fossil. Phil. Trans. Roy. Soc. Lond. Ser. B, **312**:379-430.

Wiley, E. (1981): Phylogenetics: The Theory and Practice of Phylogenetic Systematics. John Wiley, New York, 439 pp.

Williston, S. W. (1925): The Osteology of Reptiles. Cambridge, 300 pp.

Wu, X. C. (1986): A new species of Dibothrosuchus from Lufeng Basin. Vert. PaLas., **24** (1):43-62.

Young, C. C. (1948): A review of Lepidosauria from China. Amer. J. Sci., 246:711-719.

Young, C. C. (1951): The Lufeng saurischian fauna in China. Palaeont. Sinica. New Ser. C, 13:1-96.

Young, C. C. (1982): A new fossil reptile from the Lufeng Basin, Yunnan, China. In Selected Works Of Young C. C:36-37. Beijing, China: Science Press, Academia Sinica.

ABBREVIATIONS USED IN FIGURES

(Skull)

a	angular
adch	adductor chamber
afeo	articular facet for exoccipital
afn	articular facet for nasal
ar	articular
artc	articular complex
asp	ascending process
bcc	braincase cavity
bo	basioccipital
bpt	basipterygoid process
bptj	basipterygoid joint
bs	basisphenoid
c	coronoid
ca	cavity
ccoc	central cavity of otic capsule
co	conch
con	condyle
crint	crista interfenestralis
crp	crista prootica
crt	crista tuberalis
d	dentary
dep	depression
dp	process of dentary
dps	descending process of squamosal

dt	dentary teeth
ec	ectopterygoid
edd	endolymphatic duct
edf	endolymphatic foramen
eo	exoccipital
ep	epipterygoid
est	extrastapes
f	frontal
fim	fissure metotica
fm	foramen magnum
fo	fenestra ovalis
fop	fossa for paraoccipital process
fos	fossa
fr	fenestra rotundum
hy	hyoid bone
inch	inner choana
isp	interorbital septum
j	jugal
lar	lagenar recess
lf	lacrimal foramen
lsc	lateral semicircular canal
m	maxilla
meca	middle ear cavity
meck	Meckel's cartilage
meckc	Meckel's canal
mssf	medial shelf of supratemporal fenestra
mwb	membrane wall of braincase

n	nasal
ocr	occipital recess
ops	opisthotic
otc	otic capsule
otp	otic process
p	parietal
pa	parasphenoid
paf	parietal foramen
pal	palatine
palp	palatal process
palq	palatoquadrate
par	prearticular
paro	paraoccipital process
patr	lateral row of large palatine teeth
plr	perilymphatic recess
pm	premaxilla
po	postorbital
pof	postfrontal
ppp	posterodorsal process of premaxilla
ppsq	posterior process of squamosal
prf	prefrontal
pro	prootic
prq	pterygoid ramus of quadrate
psc	posterior semicircular canal
pt	pterygoid
ptf	pterygoid flange
ptfr	transverse row of large teeth on pterygoid flange
ptp	process of pterygoid

q	quadrate
qj	quadratojugal
qjf	quadratojugal foramen
qrp	quadrate ramus of pterygoid
rap	retroarticular process
rcc	recess crus commune
rvj	recess vena jugalaris
sa	surangular
sc	semicircular canal
so	supraoccipital
sof	subtemporal fenestra
sq	squamosal
st	supratemporal
sta	stapes
stfp	stapedial footplate
sty	scala tympani
sbf	subtemporal fenestra
sof	suborbital fenestra
sve	scala vestibuli
ty	tympanum
ung	unossified gap
v	vomer
V, VII, VIII, IX, X and XII	foramina for cranial nerves
V1, V2 and V3	branches of the Vth nerve

(Postcranial Skeleton)

as	astragalus
at	atlas
ax	axis
ca	calcaneum
cr	coracoid
F	femur
Fi	fibula
H	humerus
i	intermedium
ic	intercentra
lc	lateral centrale
mc	medial centrale
pi	pisiform
R	radius
r	radiale
sc	scapular
scr	sacral ribs
T	tibia
trg	transverse grooves
u	ulnar
U	ulna
i--v	metacarpals and metatarsals
1--5	distal carpals and tarsals

ABBREVIATIONS USED FOR MUSCLES

AP	aponeurosis
BAP	basal aponeurosis
DM	depressor mandibulae
MA	mandibular artery
MAME	adductor mandibulae externus
MAMEM	adductor mandibulae externus medialis
MAMEP	adductor mandibulae externus profundus
MAMES	adductor mandibulae externus superficialis <u>sensu stricto</u>
MAMI	adductor mandibulae internus
MAMP	adductor mandibulae posterior
MCID	constrictor internus dorsalis
MIM	intermandibularis
MIMP	intermandibularis posterior
MLAO	levator anguli oris
MLB	levator bulbi
MLPT	levator pterygoidei
MPPT	protractor pterygoidei
MPSTP	pseudotemporalis profundus
MPSTS	pseudotemporalis superficialis
MPTA	pterygoideus anterior
MPTAT	pterygoideus atypicus
MPTM	pterygo-mandibularis
MPTP	pterygoideus posterior
MPTT	pterygoideus typicus

MRAO	retractor anguli oris
RPS	rictal plates
TA	temporal artery
TFA	temporal facia