CRANIAL SOFT ANATOMY
AND
FUNCTIONAL MORPHOLOGY
OF A
PRIMITIVE CAPTORHINID REPTILE

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ABSTRACT

Superb specimens of the early Permian captorhinomoprh reptile *Eocaptorhinus laticeps* reveal nerve and blood vessel canals and muscle scars that permit reconstruction of the soft anatomy of the head.

The cranial arterial systems of primitive and modern reptiles were grossly similar while the venous systems differed considerably. Palatal sinuses in captorhinomorphs drained anteriorly through prepalatal foramina into the orbitonasal veins and orbital sinuses. In more advanced saurian reptiles the palate was drained posterodorsally through large suborbital fenestrae into the pterygoid veins.

The captorhinomorph M. adductor mandibulae was divided into partes externa (subdivided into partes superficialis, media, and profunda), interna, (subdivided into M. pseudotemporalis and M. pterygoideus), and posterior. The M. constrictor dorsalis was well developed. This complex musculature operated a metakinetic skull. This movement between the skull roof and braincase synchronized mandibular and maxillary impact on prey reducing prey acceleration, unnecessary energy expenditure, and prey escape. The primitively metakinetic skulls of early captorhinomorphs, millerosaurs, diapsids, and procolophonids had vertical occiputs with large post-temporal fenestrae. Akinesis resulting from size increase in pareiasaurs and advanced captorhinids did not affect this pattern. Akinesis resulting from strengthening the skull of early carnivorous pelycosaurs led to the characteristic steeply sloped, plate-like occiput with small post-temporal fenestrae.

RESUME

Il a été possible d'observer sur de magnifiques spécimens de *Eocaptorhinus laticeps*, Reptile captorhinomorphe du Permian inférieur, les canaux des nerfs et vaisseaux sanguine ainsi que les traces d'insertion musculaire; ceci a permit de reconstruire l'anatomie des structures molles de la tête.

Les systèmes artériels crâniens des Reptiles primitifs et modernes sont grossièrement similaires tandis que les systèmes veineux différent considerablement. Chez les captorhinomorphs, les sinus palataux passent vers l'avant, à travers les foramens prepalataux dans les veines orbitonasales et les sinus orbitaires. Chez les Reptiles sauriens plus évolués, le palais était drainé posterodorsalement à travers de grandes fenêtres sous-orbitaires dans les veines ptérygoides.

Le *M. adductor mandibulae* des captorhinomorphes était divisé en *partes externa* (subdivisée en *partes superficialis, media, et profunda*), *interna* (subdivisée en *M. pseudotemporalis* et *M. pterygoideus*), et *posterior*. Le *M. constrictor dorsalis* était très developé. Cette musculature complexe faisait fonctionner un crâne métakinétique. Ce mouvement entre le toit crânien et la boite crânienne synchronisait l'impact maxillaire et mandibulaire sur la proie, réduisant d'une part l'acceleration transmise à la proie, d'autre par la deprese énergetique non nécessaire ainsi que les possibilites d'échapper de la proie. Les crânes primitivement métakinétique des Captorhinomorphes primitifs Millerosaures, Diapsides, et Procolophonidés, ont des occiputs verticaux a relativement grandes fenêtres post-temporales. L'akinétisme resultant de l'accroissement de la taille chey les Paréiasaures et les Captorhinides évolués n'a pas modifié ce plan. L'akinétisme résultant du

renforcement du crâne chez les Pélycosaures carnivores primitifs même à un occiput caractéris à petites fenêtres post-temporales.

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PREFACE

The science of vertebrate paleontology has long revolved around the simple collection and description of fossil bones. Only in the past decade has a concerted effort been made to examine the biological aspects of ancient animals. To date such studies have been confined principally to fossil mammals, the anatomy of which is grossly similar to that of many living mammal taxa. Amongst reptiles only dinosaurs with their generally bird-like morphology and advanced therapsids with their mammal-like anatomy have been studied even superficially. No concerted effort has been made to study the complex non-osteological anatomy of one of the most primitive groups of fossil reptiles, the Captorhinomorpha.

The best preserved captorhinomorph reptile known is *Eocaptorhinus laticeps* of the relatively specialized family Captorhinidae from the lower Permian Wellington Formation of northcentral Oklahoma (Heaton, M.Sc. thesis, McGill Univ., 1975). Its skull and mandibles have revealed many channels, canals, and foramina formerly occupied by nerves, arteries, and veins as well as large scarred areas from which muscles formerly originated or onto which they inserted. No study of the cranial circulatory system of a fossil reptile has ever been attempted. In fact, fewer than a half dozen detailed studies of the cranial circulatory systems of all types of modern reptiles have been pursued and these mostly during the middle of the nineteenth century. Primitive reptiles were sufficiently heavily ossified that many veins and arteries passed through foramina and canals in the bone of the skull thus allowing reconstruction of the cranial circulatory system with a surprising degree of confidence. It is believed that a knowledge of the cranial circulatory system of captorhinomorph reptiles is essential if an understanding of the stages and processes leading to the diverse cranial circulatory patterns of later reptiles and mammals is to be gained.

Reconstructions of the cranial musculature of primitive reptiles have appeared irregularly during the last sixty years. In most cases the mandibular muscles have been regarded as a single adductor or "temporalis" muscle mass. It is only with the discovery of well developed muscle origin and insertion scars in the early Permian captorhinids *Eocaptorhinus laticeps* and *Captorhinus aguti* that separate muscle segments and slips can be reconstructed. Such reconstructions have never been attempted for primitive reptiles.

While the mandibular adductor musculature of modern reptiles seems to be grossly similar to what is believed to have existed in captorhinomorphs the adductor musculature of modern mammals is considerably different. If the complex changes that occurred in the modification of the mammalian lower jaw and the origin of the mammalian inner ear are to be understood completely, the structure of the muscles in the most primitive reptiles must be outlined completely. Likewise if the evolutionary events that accompanied the amphibian-reptilian transition, with its change from an aquatic piscivorous feeding mode to a terrestrial insectivorous mode, are to be appreciated fully, the cranial anatomy of the earliest reptiles, the end products of this transition, must be outlined in detail. The rapid diversification of reptiles after their first appearance was as much due to the functional advantages afforded by the newly evolved mandibular adductor musculature to a terrestrial insectivore and to the the high degree of variability and adaptability of the many segments of this muscle mass to perform different functions as it was to the development of the amniotic egg.

Cranial kinesis has long been recognized as a curious feature typical of many modern lizards and a few advanced fossil reptiles. Many different hypotheses have been advanced to explain why this system of relative movement of different segments of the skull and mandibles occurs with only a few meeting any degree of acceptability. Only Versluys (1912) and Bock (1963) expected that a simple form of cranial kinesis, metakinesis, movement between the skull roof (maxillary segment) and braincase (occipital segment), was a primitive characteristic of reptiles. The realization that metakinesis was not only present as a primitive characteristic of the earliest reptiles but also was an extremely important factor in the adaptation of reptiles to a terrestrial insectivorous feeding mode is essential if the relationships amongst early reptiles and the rapid radiation of these early reptiles during the late Carboniferous and Permian are to be understood.

Each section of this thesis has been prepared as a separate publishable manuscript. As such, a complete literature review is included in each section.

CRANIAL CIRCULATORY SYSTEM
OF A
PRIMITIVE CAPTORHINID REPTILE

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Abstract

The cranial arterial system of most modern reptiles is based on a two part division of the internal carotid into a dorsal stapedial and a ventromedial palatal distributary system. The system in primitive, captorhinomorph reptiles was similar with minor exceptions. There were three branches of the inferior orbital artery (stapedial system), two intraosseous (supramaxillary and superior alveolar arteries) and one extraosseus (maxillary artery). Turtles are the least specialized modern reptiles in this region for they have retained the superior alveolar and supramaxillary arteries but have lost the maxillary artery. In rhynchocephalian *Sphenodon* and in acrodont lizards the intraosseous supramaxillary and superior alveolar arteries are present and the maxillary lost. In pleurodont lizards, extensive reduction of the bone of the maxilla has left an extraosseous supramaxillary artery with the maxillary and superior alveolar arteries being lost or indistinguishable.

The venous system of captorhinomorph reptiles was considerably more primitive than that of any modern reptile. Captorhinomorphs apparently drained blood from the palate anteriorly into the large orbitonasal vein thence posterodorsally into the orbital sinus before leaving the head through the vena capitis lateralis. In modern reptiles, blood from the palate is conducted posterodorsally through large suborbital fenestrae into the pterygoid vein, by-passing the orbital sinus. *Sphenodon* exhibits an intermediate condition in which palatal blood can drain into both the pterygoid vein and into the orbitonasal vein. In lizards, the orbitonasal

vein is greatly reduced so that palatal blood drains only into the pterygoid vein. Pelycosaurs possessed no palatal foramina through which blood could be transported to either the pterygoid vein or the orbitonasal foramen. Palatal drainage may have been accomplished through an external mandibular vein, the precursor of the mammalian deep facial vein and proximal portion of the external facial vein.

FIGURES

Fig. 1. *Eocaptorhinus laticeps*. Skull reconstruction.

Fig. 2. Reconstruction of the cranial arterial systems of *Eocaptorhinus*, *Sphenodon*, and a typical lizard.

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Fig. 4. Reconstruction of the cranial circulatory system of *Eocaptorhinus* in ventral aspect.

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Fig. 14. *Eocaptorhinus laticeps*. Palate in ventral aspect.

THE CRANIAL CIRCULATORY SYSTEM OF A CAPTORHINID REPTILE

Introduction

The study of the origin and diversification of the earliest reptiles is both fascinating and frustrating. The fossil record is meagre, providing brief glimpses of an evolving fauna through fragments of bone from many scattered sites. Although reptiles first appeared in the Middle Pennsylvanian (300 million years ago), the first major reptilian fauna that is currently well known did not appear until the Late Pennsylvanian (290 million years ago). By this time three distinct groups of reptiles were represented, a seemingly primitive anapsid (no temporal fenestrae) captorhinomorph lineage, a synapsid (one lateral temporal fenestra) pelycosaur lineage, and a diapsid (one dorsal and one lateral temporal fenestra) eosuchian lineage. It is known that the diapsid line expanded to give rise to modern *Sphenodon*, lizards, snakes, crocodiles, and birds as well as to the extinct dinosaurs, and that the synapsid line eventually gave rise to mammals. The exact relationships of the anapsid reptiles of the sub-order Captorhinomorpha have remained obscure although they are thought to be closely related to the diapsid lineage. Although modern turtles are essentially anapsid, few researchers have considered them to be captorhinomorph derivatives although this has been considered a possibility by Carroll (1969b and c; Carroll and Gaskill, 1971; Clark and Carroll, 1973). Because of their unique position close to the origin of all modern diapsid reptiles and, according to Carroll's theories, turtles, knowledge of captorhinomorph anatomy is extremely important to the development of modern theories on the evolutionary diversification and subsequent radiation of reptiles.

Amongst the Captorhinomorpha, the members of the somewhat specialized family Captorhinidae are known from the most complete material. The species *Eocaptorhinus laticeps* (Fig. 1) from the Early Permian Wellington Formation of northcentral Oklahoma and the Belle Plains and Clyde Formations of northcentral Texas, is a primitive captorhinid whose remains are perhaps the best preserved of any Paleozoic reptile so far discovered (Heaton, 1975, 1978) (Fig. 1). Although fossil captorhinomorphs have been discovered in earlier deposits, including some earlier captorhinids, none is well enough preserved to provide a comparable amount of osteological detail as that available in *Eocaptorhinus*. This form is thus of great significance in determining the basic anatomical characteristics of the most primitive group of true reptiles and in interpreting the ancestry and early phylogenetic history of reptiles. Its fine osteological details have been studied by Heaton (1975, 1978) as has its mandibular adductor musculature.

The development of an accurate reconstruction of the cranial circulatory system of *Eocaptorhinus laticeps* is hindered by a paucity of published information on the development of this system in modern reptiles. Older papers such as Bojanus' (1819-21) study of the anatomy of the turtle *Emys orbicularis ("Testudo europeae")* and Corti's (1847) investigation on the circulatory system of *Varanus griseus (Psammosaurus griseus)* are of chiefly historical importance. While Rathke (1856, 1857, 1863) made important contributions to the literature on the basal divisions of the carotid arches in many reptiles and mammals, it was not until 1907 that a complete system was studied. In that year Bruner produced an excellent study of the cranial venous system of a lizard based primarily on *Lacerta agilis* with brief notes on turtles and snakes. O'Donoghue (1920) studied the circulatory system of *Sphenodon punctatus* including both the arterial and venous systems

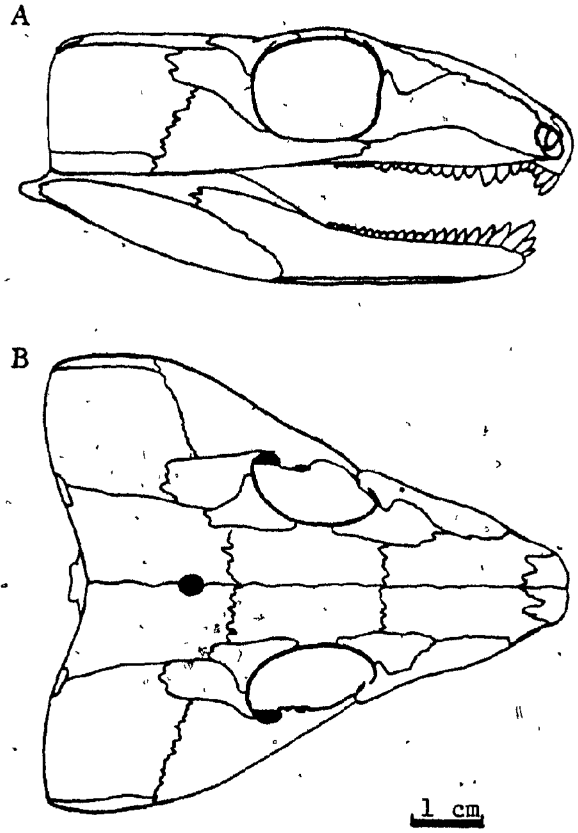

Figure 1. *Eocaptorhinus laticeps*. a) Lateral aspect. b) Dorsal aspect. Reconstruction. Natural size.

of the head. It was not until 1956 that a complete description of the cranial arterial system of a specific lizard, *Ctenosaura pectinata,* was produced by Oelrich. Even less has been done on turtle cranial arterial systems. Albrecht (1967) extended McDowell's (1961) study of the major cranial arteries in testudinid, kinosternid, and trionychid cryptodires. A single paper by Hochstetter (1906) on the circulatory system of crocodiles is extremely difficult to obtain in North America. The only paper to date dealing with a comprehensive and truly comparative study of the cranial arterial system of modern reptiles was published by Shindo in 1914. No such study of the venous systems has been made.

The reconstruction of soft anatomy in fossil reptiles is sure to excite diverse and often heated discussion on the practicality or advisability of such an approach in the study of vertebrate fossils. Some workers prefer to dismiss all or most such reconstructions as meaningless excursions into anatomical analogizing and circular reasoning while others maintain that a good knowledge of the anatomy of living forms accompanied by much careful and logical reasoning, can lead to accurate interpretations (Barghusen, 1968, 1973). The former attitude, while undoubtedly safer, will not advance our knowledge or understanding of fossil reptiles nor will it promote the conception of fossil vertebrates as living, functioning organisms in their own time rather than just as osseous remains.

Not all of the arteries or veins of *Eocaptorhinus laticeps* can be identified with equal confidence. The presence of well formed foramina and canals through the skull bones of fossil forms in positions that have the same anatomical relationships to the cranial elements as are exhibited by modern reptiles provide good evidence for the identification of many arteries and veins. The heavily ossified skulls of captorhinomorph reptiles lend themselves well to the identification of both blood vessel canals and the heavily scarred origins and insertions of the jaw adductor musculature. In other cases, the courses of arteries and veins through the head where they do not contact the bone must be determined by analogy with modern forms. The courses of these vessels around and through the jaw adductor musculature is of particular importance. Careful reconstruction of these muscles in fossil reptiles allows the path of the arteries and veins to be determined with reasonable accuracy.

In order to provide a firm basis from which to discuss the cranial circulation system in *Eocaptorhinus laticeps*, a number of modern reptile species including the lizards *Iguana iguana* (Iguanidae), *Ctenosaura* sp. (Iguanidae), *Gekko gecko* (Gekkonidae), and *Tupinambis nigropunctatus* (Teiidae) were dissected. The modern testudinid cryptodire turtle *Pseudemys scripta* was also examined so that variation from the lepidosaurian pattern might be exposed. *Pseudemys* is a typical testudinid and is thus relatively primitive in its cranial arterial system compared to many other turtles (McDowell, 1961; Albrecht, 1967; Gaffney, 1972). It revealed a pattern similar in general form to that of lepidosaurs. The highly specialized skull structure of crocodilians has influenced the positions of many blood vessels, leading to the development of secondary anastomoses, particularly of the arteries, that have rerouted blood flow through the head. Hochstetter's (1906) study of the cranial circulatory system of crocodilians is apparently the only one to have been made.

Since the cranial blood vessel patterns of a diverse assemblage of modern reptiles including *Sphenodon* (O'Donoghue, 1920), lizards, and some relatively primitive turtles, are generally consistent, it is safe to assume that a primitive reptile such as *Eocaptorhinus* had a cranial circulatory system that was based on a similar pattern.

Cranial Arterial System

The most comprehensive reviews of the cranial arterial systems of modern reptiles have been produced by Bojanus (1819-21) on the turtle *Emys*, Corti (1847) on the lizard *Varanus*, O'Donoghue (1920) on the rhynchocephalian *Sphenodon*, and Oelrich (1956) on the lizard *Ctenosaura*. Rathke (1856, 1857, 1863) studied the primary divisions of the internal carotid in numerous modern lizards and snakes while McDowell (1961) and Albrecht (1967) have examined the development of these branches in some modern cryptodire turtles. To date there have been no studies of the cranial arterial system in primitive reptiles with the exception of Price's (1935) brief mention of the arteries passing through or contacting the braincase in the captorhinid *Captorhinus aguti*. In the closely related form *Eocaptorhinus laticeps* many arteries pass through osseous canals or extend along well marked channels in the bone of the skull (Heaton, 1975, 1978), thus allowing reconstruction of the cranial arterial system with considerable confidence.

Oxygenated blood is pumped from the heart anteriorly through a common carotid[1] which bifurcates to form a prominent internal carotid and a smaller external carotid (Bojanus, 1819-21; Corti, 1847; Rathke, 1856, 1857, 1863; O'Donoghue, 1920). Blood from the external carotid circulates to the hyoid and intermandibular musculature while that from the internal carotid passes to the head through two main branches, the palatal artery and the stapedial artery. The palatal artery is a relatively small anterior continuation of the internal carotid that provides blood to the brain and the ventral surface of the palate. The larger stapedial artery, which is lost in some turtles

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[1] A carotid is, by definition, an artery and, to avoid unnecessary redundancy, should never be called the carotid artery.

(McDowell, 1961; Albrecht, 1967), extends vertically into the adductor chamber to supply the adductor musculature, the orbit, the snout, the dorsal surface of the palate, and the skin through its many branches.

Carotis internus (CI)

The internal carotid forms the main blood supply to the head of *Sphenodon,* lizards, snakes, and turtles. In crocodilians it is supplemented by a connection with the external carotid. In modern reptiles the internal carotid approaches the head, lateral to the oesophagus, ventrolateral to the braincase (Figs. 2 and 3). At the level of the third cervical vertebra, before entering the head, it divides into two branches, the large dorsal stapedial artery (AST) and the smaller ventral continuation of the internal carotid. In *Sphenodon* and lizards the internal carotid continues anteriorly, as a vessel of greatly reduced diameter, along the lateral surface of the basisphenoid to enter the vidian canal with the vidian (palatine) ramus of the facial nerve. In *Sphenodon,* the course of the internal carotid runs anteroventrally in a prominent groove on the lateral surface of the basisphenoid. In turtles, the internal carotid enters the internal carotid canal soon after the separation of the stapedial artery and is joined anteriorly, within the canal, by the vidian nerve. In crocodilians, the greatly expanded braincase and modified quadrate have enclosed the internal carotid posterior to the divergence of the stapedial artery.

In *Eocaptorhinus,* the internal carotid appears, judging by the diameter of the stapedial foramen and the vidian sulcus through which its branches passed, to have been a large artery. The course of the stapedial artery and the anterior continuation of the internal carotid extended anteriorly along the ventral surface of the stapes in the angle between the footplate

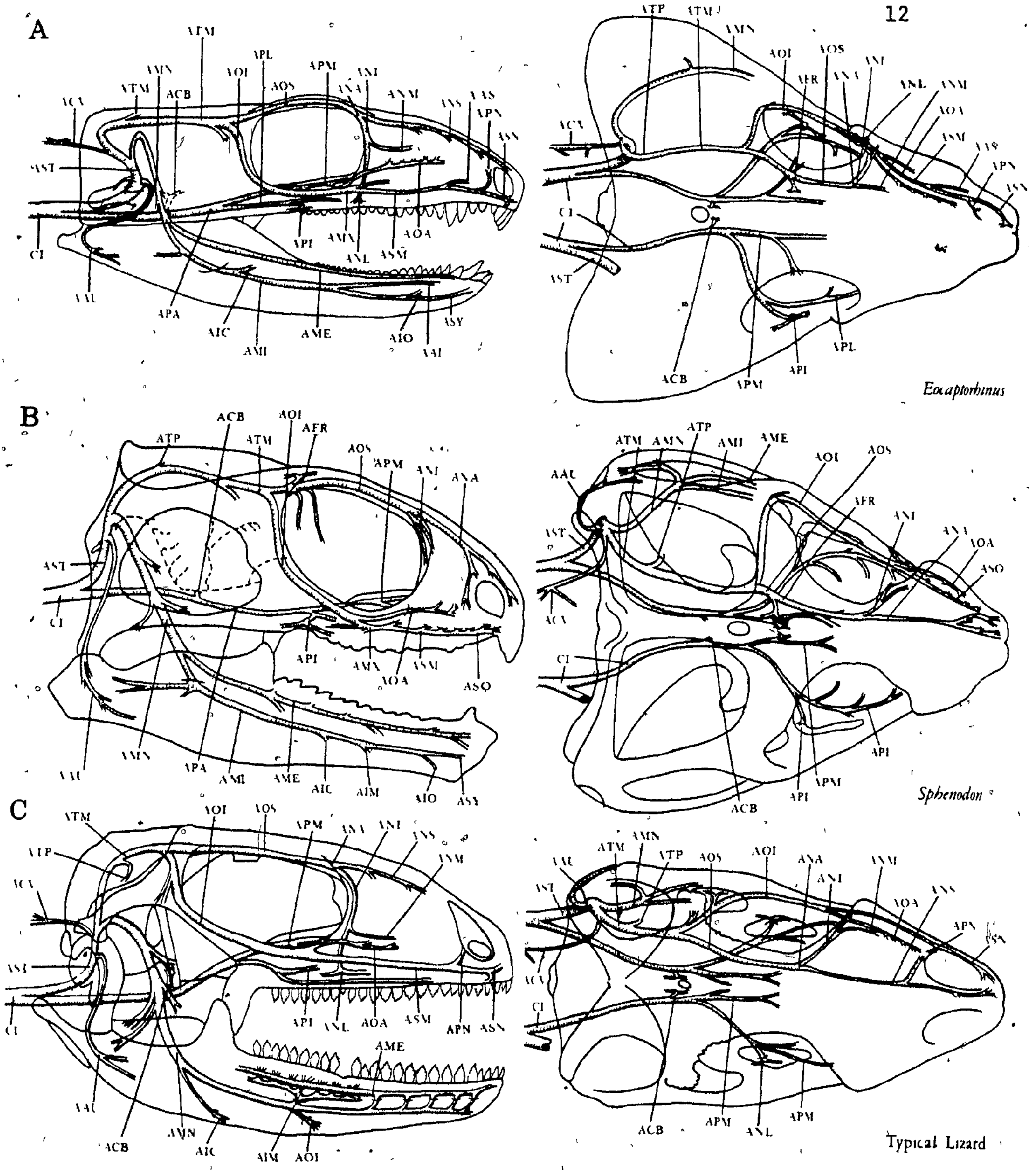
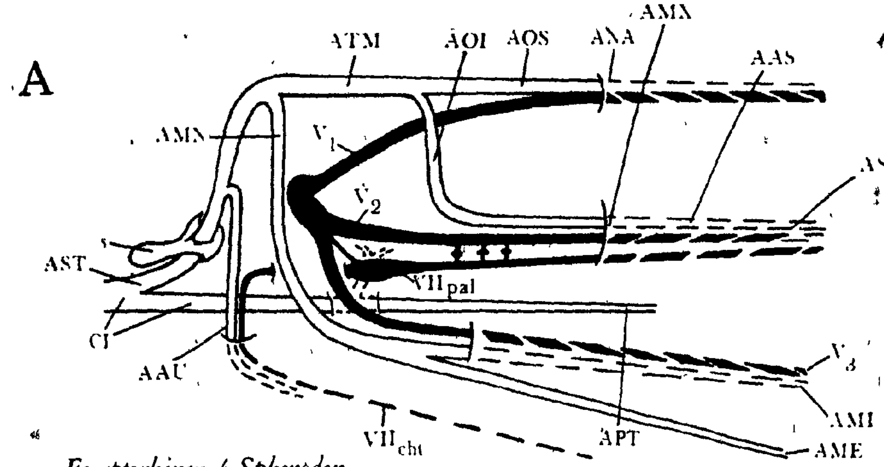


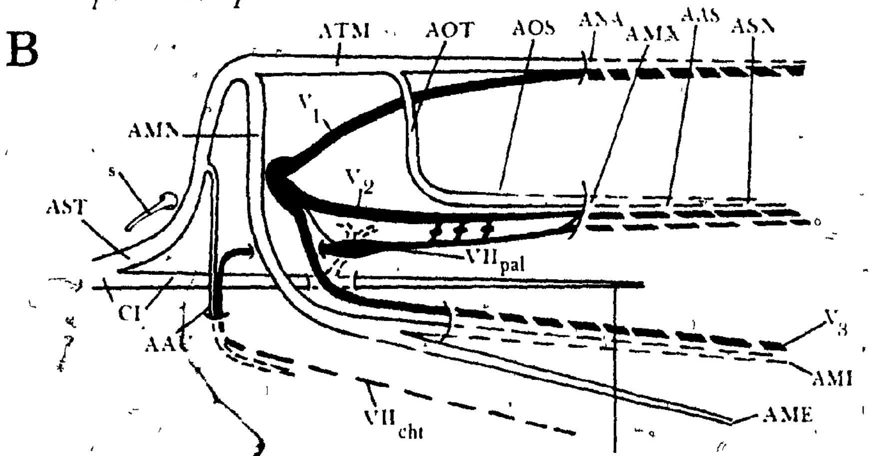
Figure 2. Reconstructions of the arterial systems in dorsal and lateral aspect of *Eocaptorhinus*, *Sphenodon*, and a typical lizard (*Iguana* outline representative).

A



Eocaptorhinus / Sphenodon

B



Typical Lizard

Figure 3. Schematic reconstruction of major arteries in *Eocaptorhinus* and *Sphenodon* and in a lizard.

and the columella. The stapedial artery turned dorsally (Fig. 4, 5) while the internal carotid ran further anteriorly and slightly medially within a narrow, shallow groove on the lateral surface of the parasphenoid where it apparently lay beneath an ensheathing mucous epithelium, as in modern reptiles, dorsal to the crista ventrolateralis and ventral to the grooves for the vidian (palatine) ramus of the facial nerve and the vena capitis lateralis. At the point where the grooves for the internal carotid and the vidian nerve intersected, a major trunk of the internal carotid, the palatine artery (APL), continued anteriorly through the vidian sulcus and a much smaller vertical branch entered the posterior internal carotid foramen and canal as the cerebral artery (Fig. 2). The vidian sulcus has a uniform width of about 0.5 mm and the stapedial foramen a diameter of about 2 mm thus reflecting the noticeable difference in the size between the two major divisions of the internal carotid.

Arteria stapedialis (AST)

The stapedial artery is the chief conduit of blood from the internal carotid to the muscles and organs of the head in *Sphenodon*, lizards, and many genera of turtles. Some turtles (kinosternids, trionychids) have greatly reduced the stapedial artery and nourish the majority of the structures of the head through the palatine artery. Amongst modern lepidosaurs, the presence of a stapedial foramen traversed by the stapedial artery, in the specialized ascalobotan lizards *Dibamus* and *Anelyatropsis* of the family Dibamidae, is considered to be a retained primitive character (Underwood, 1971; Greer, 1976). In *Sphenodon*, gekkonid and pygopodid lizards, and snakes, the stapedial artery passes anterior to the stapes while in all other lizards, it passes posteriorly (Greer, 1976). Similarly, the stapedial

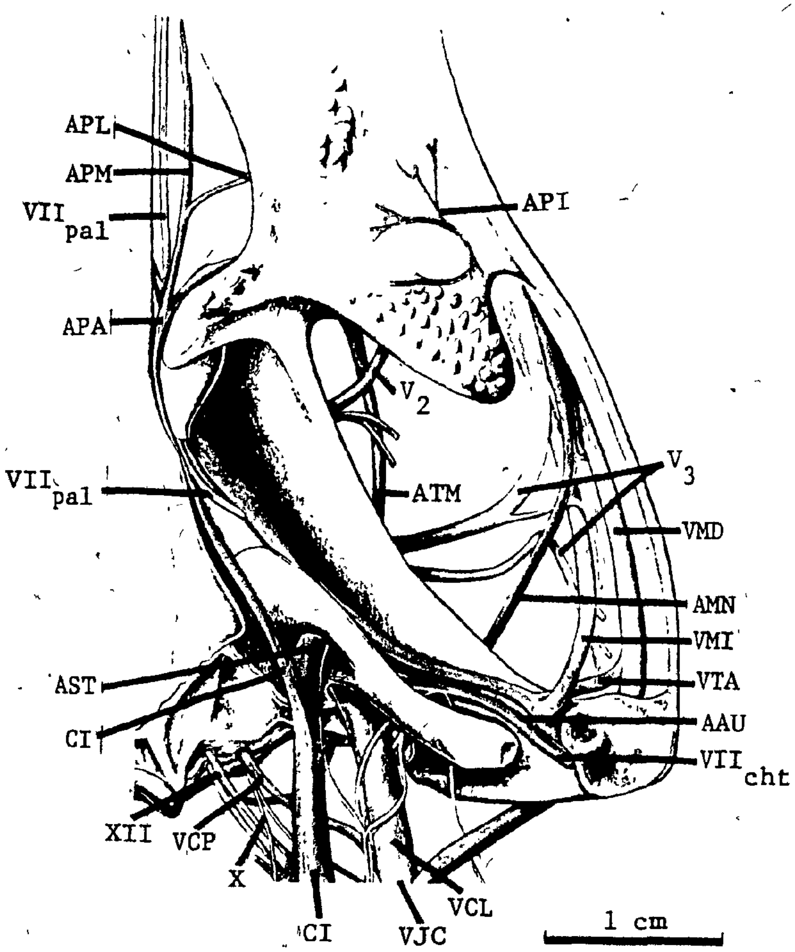


Figure 4. *Eocaptorhinus laticeps*. Skull in ventral aspect showing arterial, venous, and cranial nervous systems. Reconstruction.

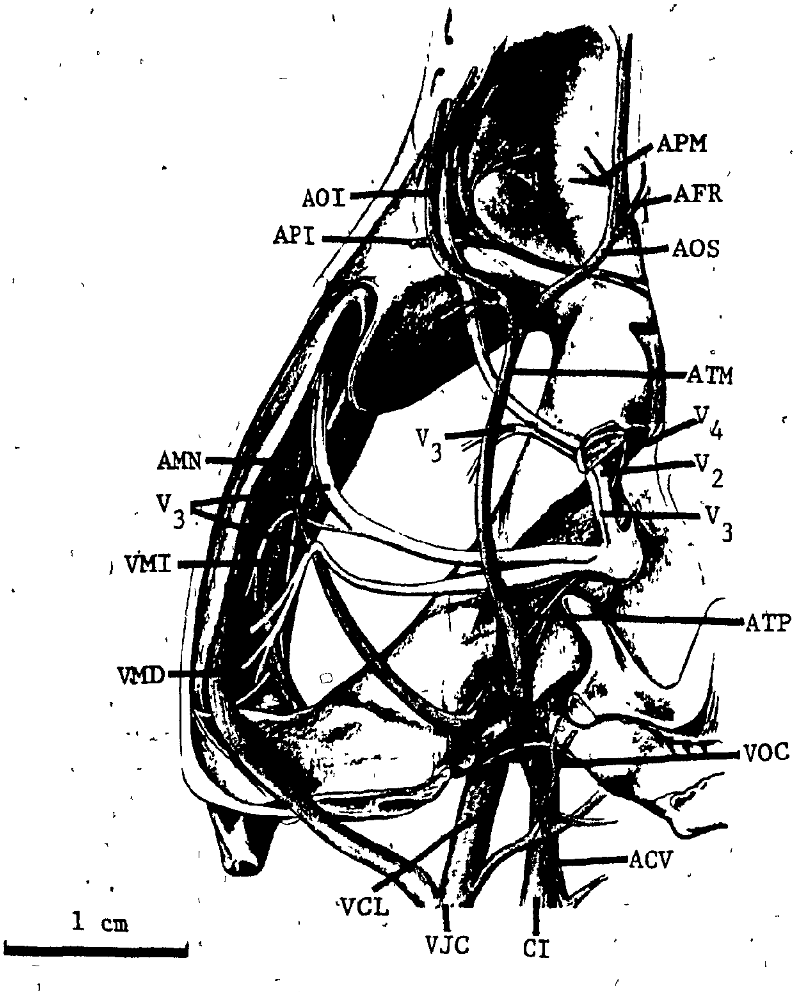


Figure 5. *Eocaptorhinus laticeps*. Skull in dorsal aspect showing arterial, venous, and cranial nervous systems. Reconstruction.

artery of turtles and crocodilians lies posterior and dorsal to the stapes (Shindo, 1914).

In *Eocaptorhinus*, the stapedial artery entered the large (2 mm diameter) stapedial foramen by way of a short groove in the ventral surface of the stapes (Figs. 4 and 6). It passed vertically through the foramen to emerge anterior to the dorsal process of the stapes. Within the stapedial foramen it gave off a tiny ventrolaterally directed columellar twig that penetrated into a tiny foramen in the body of the columella of the stapes (Price, 1935; Heaton, 1975, 1978). The stapes is perforated by the stapedial foramen in all known captorhinomorphs. The post-arterial segment of the columella of the stapes of *Eocaptorhinus*, which includes the dorsal process, is much more robust than the pre-arterial portion, in contrast to the form seen in *Hylonomus* (Carroll, 1964) and *Paleothyris* (Carroll, 1969a) where the pre- and post-arterial sections are of equal size.

In most modern reptiles, as the stapedial artery passes the dorsal limit of the stapes, the stapedial artery divides into a small auricular branch (AAU) and a large temporal artery (ATM). A similar pattern is believed to have existed in *Eocaptorhinus*.

Arteria auricularis (AAU)

Auricular arteries have been described in both *Sphenodon* (O'Donoghue, 1920) and in lizards (Corti, 1847; Oelrich, 1956) although their apparently different structure puts their supposed homologies in question. In *Sphenodon*, where the stapedial artery lies anterior to the stapes, the auricular artery arches posterodorsally over the stapes, although O'Donoghue (1920) is not clear on this latter point, apparently medial to the squamosal processes of the extracolumella of the stapes (Versluys, 1898, 1904; Gans

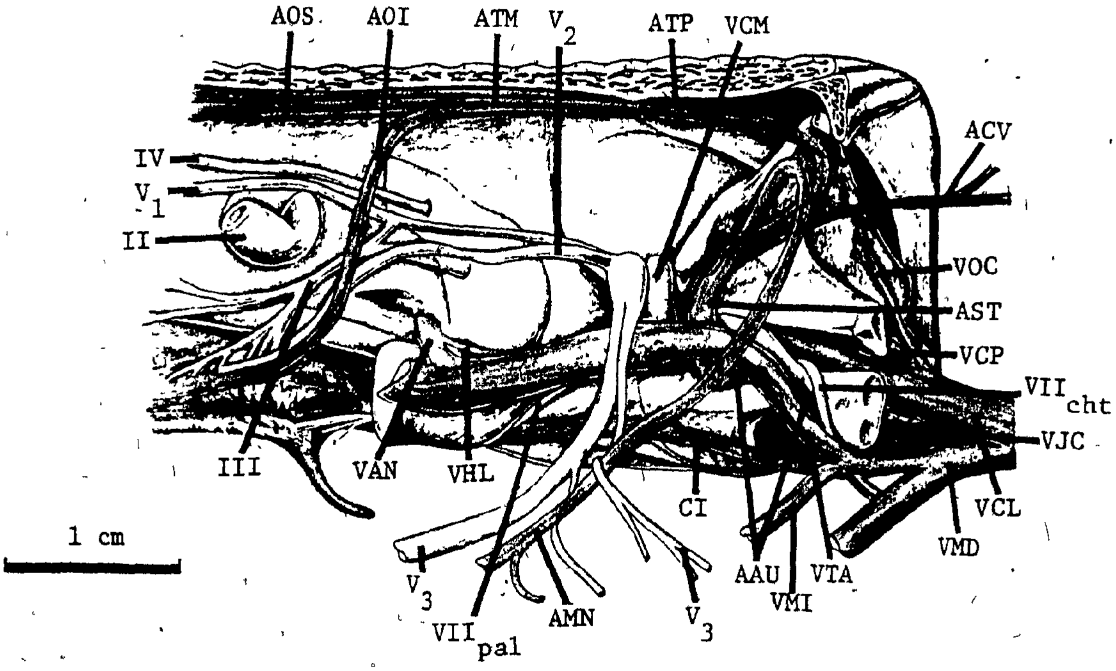


Figure 6, *Eocaptorhinus laticeps*. Skull in lateral aspect showing arterial, venous, and cranial nervous systems. Reconstruction.

and Wever, 1976) before extending vertically down the posterior surface of the tympanic cavity accompanied by the chorda tympani ramus of the facial nerve (O'Donoghue, 1920). This description appears to be incorrect since the chorda tympani nerve in reptiles is pre-tympanic (Goodrich, 1915, 1930; Hotton, 1960), passing down the anterior wall of the tympanic cavity on the posterior surface of the quadrate. It appears most likely that the auricular artery of *Sphenodon* accompanies the hyomandibular ramus of the facial nerve (not the chorda tympani) across the posterior surface of the tympanic sac. In lizards, the auricular artery is quite complex, consisting of three major rami (Oelrich, 1956). One ramus arches over the extracolumella and extends down the posterior face of the quadrate, a second extends laterally to the tympanic membrane, and the last extends ventrally across the posterior surface of the tympanic cavity accompanied by the hyomandibular ramus of the facial nerve (Oelrich, 1956). It is to the last of these that the auricular artery of *Sphenodon* appears to be homologous. It is possible that a pre-tympanic ramus of the auricular artery that accompanies the chorda tympani may have been missed in O'Donoghue's study (1920). Auricular arteries have not been described in either turtles or crocodilians. Whether this is a result of the absence of such arteries or the absence of detailed information about these groups of animals in general is not known.

A deep groove in the dorsal surface of the stapes anterior to the dorsal process suggests that *Eocaptorhinus* possessed an auricular artery. Examination of well preserved stapes of *Eocaptorhinus* and the closely related form, *Captorhinus*, show slight channelling on the anterior surface indicating that the auricular artery bifurcated, producing a pre-tympanic branch that accompanied the chorda tympani nerve and a post-tympanic branch that accompanied the hyomandibular ramus of the facial nerve. It is apparent that if the post-tympanic branch existed, it crossed the columella lateral to the dorsal process (Fig. 5). The sharp angle separating the stapedial formamen from the jugular canal between the dorsal process and the footplate makes it unlikely that the auricular artery passed through the jugular canal.

Arteria temporalis (ATM)

The stapedial artery of *Sphenodon* and lizards passes dorsal to the superior edge of the pterygoid lamella of the quadrate and enters the adductor chamber where it becomes known as the temporal artery. At this point it produces first a small cervical artery (ACV) and then, slightly more distally, it gives rise to the mandibular artery (AMD) before turning anterodorsally to pass through the body of the M. adductor mandibulae externus medius (Oelrich, 1956; Haas, 1973). No comprehensive study of the relationship between the cranial arteries and muscles of turtles has been published. It appears that the deep emargination of the posterior margin of the skull roof in most turtles has led to the reduction in size of the medial mass of the M. adductor mandibulae externus medius so that the temporal artery now passes medial to the remaining lateral mass, between it and the greatly enlarged M. adductor mandibulae externus profundus. Crocodilians with their even more highly specialized braincase are of little applicability to the question of the position of the temporal artery in relation to the M. adductor mandibulae superficialis.

In *Sphenodon* (O'Donoghue, 1920) and lizards (Oelrich, 1956) the temporal artery produces a short branch at or just posterior to the anterior edge of the M. adductor mandibulae externus medius that supplies the superior temporal fascia and skin covering that muscle. Anteriorly, the temporary artery runs along the lateral surface of the M. pseudotemporalis superficialis medial to the M. adductor mandibulae externus superficialis. Posterior to the orbitotemporal membrane it divides to produce an anteromedial superior orbital artery (AOS) and a ventrolateral inferior orbital artery (AOI) (Rathke, 1863; Shindo, 1914; O'Donoghue, 1920; Oelrich, 1956). The same division occurs in those turtles that retain the stapedial and temporal arteries (McDowell, 1961; Albrect, 1967).

In *Eocaptorhinus*, there is little evidence in the bone of the exact course of the temporal artery, however, both the proximal end and several branches of the distal end passed through bony foramina, in this case, the former through the stapedial foramen and the latter through the infraorbital and anterior orbital foramina. This evidence supports the assumption that the temporal artery passed through the adductor chamber as in *Sphenodon*, lizards, and most turtles. Such a position of the temporal artery is further supported by the presence of a prominent foramen which may be attributed to the temporoparietal branch of the temporal artery and which lies within the large parabolic depression identified as being associated with the M. adductor mandibulae externus medius (Fig. 7). The position of this foramen corresponds closely with the position of the temporal artery in *Sphenodon* and lizards on the one hand and *Eocaptorhinus* on the other, it appears that the temporal artery, and its short dorsal temporoparietal branch passed through the body of the M. adductor mandibulae externus medius dividing it into lateral and medial segments. The temporal artery is reconstructed as passing laterally around the M. pseudotemporalis as in *Sphenodon* (Haas, 1973), *Tupinambis*, and *Gekko* (where the M. pseudotemporalis is greatly reduced). This appears more probable than the position it has in *Ctenosaura* (Oelrich, 1956) and *Iguana* where it passes over the dorsal surface of the M. pseudotemporalis and, hence between the muscle and the parietal.

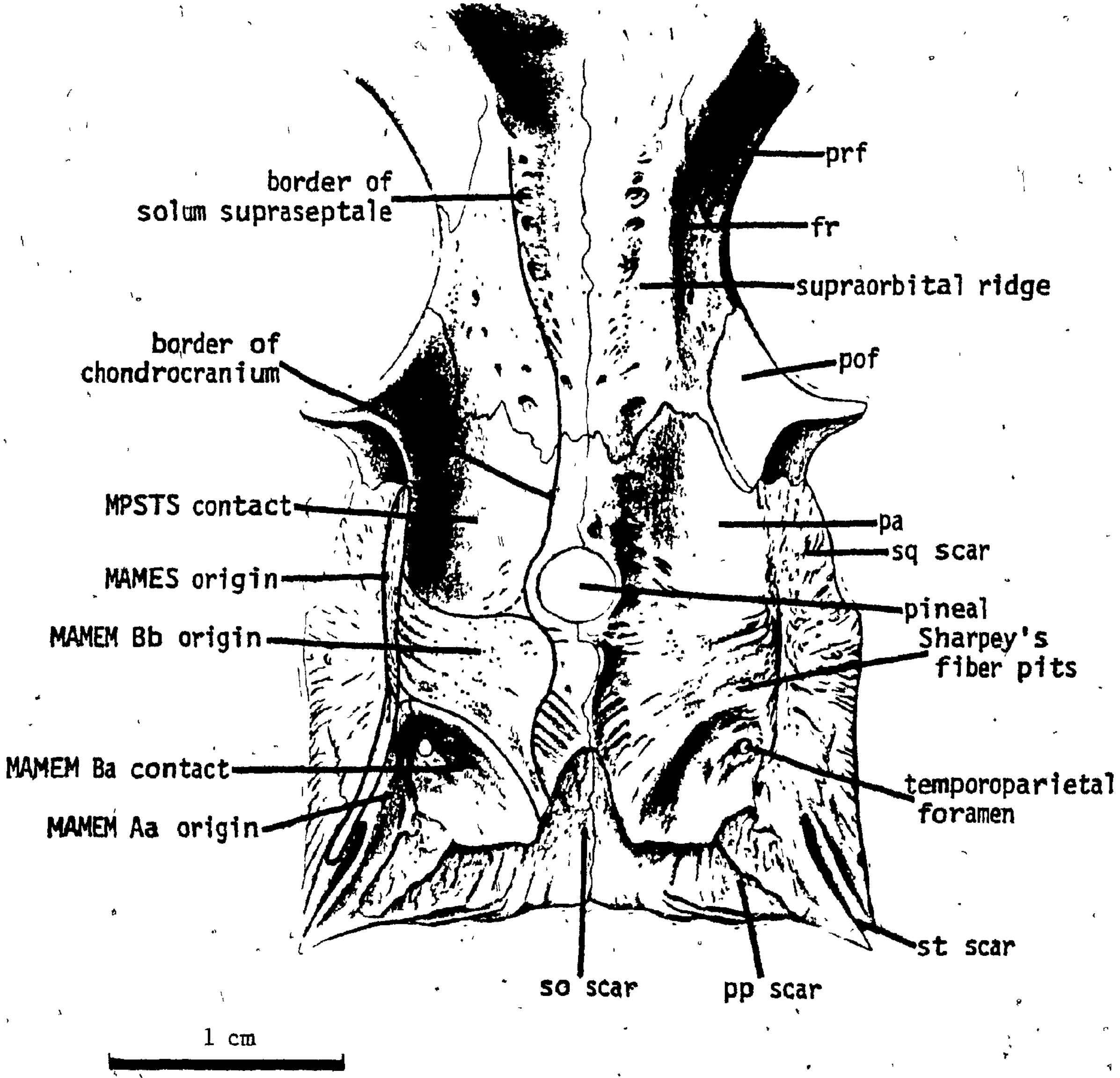


Figure 7. *Eocaptorhinus laticeps*. Skull roof in ventral aspect.

In *Sphenodon*, lizards, and most turtles, the temporal artery divides into two major branches at the anterior end of the adductor chamber, a ventral inferior orbital artery and a medial superior orbital artery. Since both the inferior orbital artery and the superior orbital arteries of *Eocaptorhinus* have left excellent evidence of their presence in the normal reptilian positions, it is probably safe to reconstruct the bifurcation of the temporal artery in the usual position just posterior to the position of the orbitotemporal membrane. The position of the orbitotemporal membrane in *Eocaptorhinus* has been determined dorsally and laterally by the orbitotemporal crest on the medial orbital rim composed of the jugal, postorbital, and postfrontal and ventrally by the orbitotemporal ridge on the dorsal surface of the pterygoid (Heaton, 1975, 1978). Medially the orbitotemporal membrane was apparently limited by the periorbital membrane and the chondrocranium.

Arteria cervicalis (ACV)

The first branch of the temporal artery is the cervical artery. It is present in *Sphenodon* and lizards, where it is usually known as the occipital artery, as well as in turtles where the term was first used by Bojanus (1819-21). Bojanus' term is used here to avoid confusion with the amphibian (anuran) occipital artery which is post-cranial, originating from the lateral dorsal aorta (Gaupp, 1899; Jarvik, 1975). In *Sphenodon*, lizards (Oelrich, 1956) and those turtles that possess temporal arteries, the cervical artery passes posterodorsally to the paroccipital process through the large post-temporal fenestra to supply the cervical musculature with blood.

Since large post-temporal fenestrae are present in *Eocaptorhinus*, just as in *Sphenodon*, lizards, and turtles, it is reasonable to expect a similar type of blood supply to the cervical musculature (Figs. 5 and 6). Crocodiles, whose post-temporal fenestrae have been reduced to narrow cartilage-filled slits (Iordansky, 1973), appear to be the only group of reptiles that have lost the cervical artery, other than those specialized turtles that have lost the temporal artery.

Arteria temporoparietalis (ATP)

O'Donoghue (1920) described a branch of the temporal artery as the "Arteria temporomasseteris" that "supplied the origin of the similarly named muscle" in *Sphenodon*. The use of the term "masseter" in reference to muscles or associated arteries is now normally restricted to work on mammalian anatomy, hence the name change here as applied to diapsid reptiles and to *Eocaptorhinus*. Haas (1973) illustrated the temporal artery of *Sphenodon* running deep within the M. adductor mandibulae mass rather than along the dorsal surface of the muscles within the superior temporal fenestra as in lizards. He does not mention the presence of a temporoparietal artery as found by O'Donoghue (1920). O'Donoghue did not note the position of the temporoparietal artery within the M. adductor mandibulae mass. Lizards appear to be similar to *Sphenodon* in the presence of a temporoparietal artery, although the whole temporal artery and its branches run along the dorsal surface of the adductor musculature. In lizards, the temporoparietal artery is given off where the temporal artery passes from between the medial and lateral divisions of the M. adductor mandibulae externus medius and extends laterally to supply the skin and lateral portion of the pars media. The general reduction of the medial portion of the pars media and its apparent replacement by the M. pseudotemporalis superficialis, particularly in the more advanced forms such as *Tupinambis* make it difficult to compare with more primitive forms. The position of the temporoparietal artery is a reliable indicator of the position of a more ventrally situated temporal artery.

In *Eocaptorhinus*, a prominent foramen penetrates the internal surface of a parabolic depression on the ventral surface of the parietal just posterior to its anterior edge (Heaton, 1975, 1978) (Fig. 7). This foramen suggests that the temporoparietal artery (Figs. 5 and 6) branches dorsally from the temporal artery to penetrate the skull roof. The position of the temporal artery and the root of the temporoparietal artery and, hence, the temporoparietal foramen are believed to indicate the line of separation between the origins of the lateral (A) and internal (B) segments of the M. adductor mandibulae externus medius just as in modern *Sphenodon* and lizards. The temporoparietal artery is presumed to have anastomosed through the vesicular bone of the parietal from which tiny arterioles originated and penetrated fine pores in the bases of the sculpture pits to supply blood to the skin. Other fine arterioles presumably supplied the muscle origins just as in modern diapsids.

Arteria orbitalis superior (AOS)

The position and form of the superior orbital artery (often termed simply the supraorbital artery) is consistent in all modern reptiles with the exception of some specialized turtles (Shindo, 1914). It branches anteromedially from the temporal artery to extend along the ventral surface of the frontal in the angle formed by the junction of the solum supraseptale and the medial edge of the crista cranii and suprorbital ridge. This same artery was termed the frontal artery by Oelrich (1956), a misnomer since it does not correspond to the frontal artery as defined by O'Donoghue

(1920). In those turtles that have retained a temporal artery, the superior orbital artery extends along the lateral surface of the crista cranii of the frontal and prefrontal. Since both the solum supraseptale of the interorbital septum and the supraorbital ridge and crista cranii are heavily ossified (Heaton, 1975, 1978) (Fig. 7), the junction between the skull roof and the anterior braincase can be reconstructed with confidence. The great similarity in the frontal-solum supraseptale junction in *Eocaptorhinus* and modern lepidosaurs, and especially in *Sphenodon*, suggests strongly that the superior orbital artery of *Eocaptorhinus* followed the intersection of these elements as it does in *Sphenodon*. The presence of numerous foramina in the frontal that carry distributory rami of the superior orbital artery in modern reptiles are also found in the frontal of *Eocaptorhinus*.

Near its origin from the temporal artery, the superior orbital artery of *Sphenodon*, lizards, and testudinid turtles produces a small medial frontal artery as may have the superior orbital artery of *Eocaptorhinus*.

Arteria frontalis (AFR)

In *Sphenodon* a short branch of the superior orbital artery supplies blood to the ventral surface of the frontal where occasionally small rami enter the body of the bone through very small foramina (O'Donoghue, 1920). In lizards, a true frontal artery as seen in *Sphenodon* has not been described. The artery described by Oelrich (1956) is actually the superior orbital (supraorbital) artery as described by Bojanus (1819-21), Shindo (1914), O'Donoghue (1920), and Albrecht (1967) in other reptiles. No specific frontal artery, as is found in *Sphenodon*, was identified in dissections of *Iguana*, *Gekko*, and *Tupinambis*. One or more fine arterial branches from the superior orbital artery enter the frontal through tiny foramina in its ventral surface. A similar arrangement is to be found in testudinid turtles (Albrecht, 1967).

It cannot be determined whether a distinct frontal artery existed in *Eocaptorhinus* as it does in *Sphenodon* or not. It is probable that, as in all modern reptiles, arterial branches originating either from a frontal artery or directly from the superior orbital artery penetrated the ventral surface of the frontal through several small foramina.

Arteria nasalis (ANA)

The nasal artery of modern reptiles, when present, is the anterior continuation of the superior orbital artery from the point where it reaches the orbitonasal foramen and passes through the ophthalmic foramen. Although the superior orbital artery enters the nasal capsule in many turtles, it is not renamed the nasal artery (Bojanus, 1819-21; Albrecht, 1967) as it is in *Sphenodon* (O'Donoghue, 1920) and lizards (Oelrich, 1956). In lizards, just as the nasal artery enters the nasal capsule, two lateral branches are produced, the superior nasal artery (ANS) and the ventrally directed inferior nasal artery (ANI). An inferior nasal artery is not present in *Sphenodon* (O'Donoghue, 1920) nor, apparently, in turtles.

In *Eocaptorhinus*, both the superior nasal artery and ventrally directed inferior nasal artery are believed to have been well developed.

Arteria nasalis superior (ANS)

In *Sphenodon* the nasal artery extends anteriorly into the snout on the dorsal surface of the nasal capsule to supply the sub-cutaneous tissue of the snout. There is no ventral ramus of the nasal artery as there is in lizards. In lizards where the nasal artery bifurcates, the two sections are given positional designations. Thus the superior nasal artery of lizards (Oelrich, 1956) is the equivalent of the entire nasal artery of *Sphenodon* and the anterior continuation of the superior orbital artery of turtles.

The nasal artery of *Eocaptorhinus* appears to have been divided as in lizards, hence the adoption of the lizard terminology. The superior nasal artery of *Eocaptorhinus* (Fig. 8a) apparently extended anteriorly from its separation from the inferior nasal artery along the ventral surface of the frontal and nasal as suggested by a shallow groove in this position. Laterally it extended across the posterior portion of the heavy antero-posterior nasofrontal ridge. The superior nasal artery presumably ran along the ventral bone surface and passed anteromedially, apparently dorsal to the orbitonasal vein, which ran within the orbitonasal canal that traversed the length of the nasal portion of the nasofrontal ridge and exited from the posterior orbitonasal foramen. The superior nasal artery is believed to have anastomosed over the whole of the internal surface of the nasal and the lachrymal as in *Sphenodon*, lizards, and turtles and, as in these forms, fed the dorsal regions of the paranasal cartilage. There are numerous small foramina in the bone of the nasal but in general there was a relatively meagre supply of blood to the skin compared with that which was transported to the parietal. This is reflected in the much lighter sculpturing of the external surface of the nasal.

Arteria nasalis inferior (ANI)

There does not appear to be a well defined inferior nasal artery in either *Sphenodon* or in turtles. In lizards the inferior nasal artery is well developed with two main divisions, a medial ramus (ANM) and a lateral

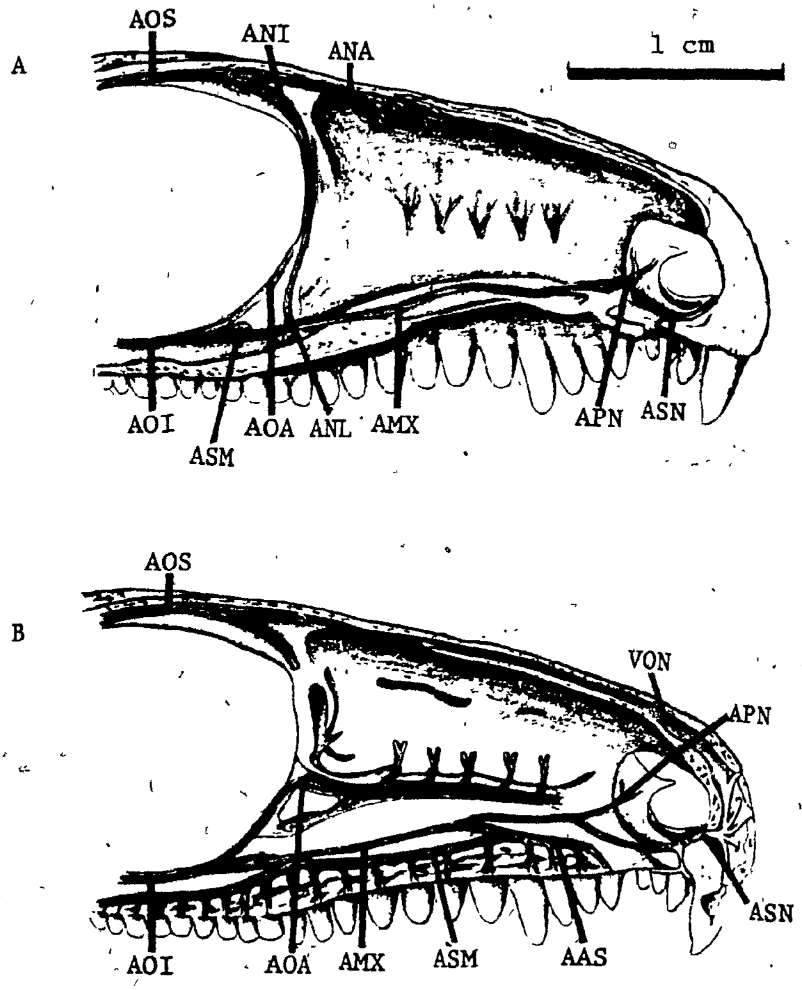


Figure 8. *Eocaptorhinus laticeps*. Snout in medial aspect. a) Showing arterioles entering nasal capsule. b) With medial surface of the lachrymal removed to show internal structure. Reconstruction.

ramus (ANL). A bifurcate inferior nasal artery is believed to have extended, in *Eocaptorhinus*, from its separation from the superior nasal artery down the posterior surface of the orbitonasal membrane as in lizards (Oelrich, 1956).

Arteria nasalis inferior ramus medialis (ANM)

In lizards the medial ramus of the inferior nasal artery continues ventrolaterally until it reaches the palatine posterior to the orbitonasal membrane where it turns rostrally and accompanies the medial ethmoidal (palatine) ramus of the facial nerve anteriorly through the medial orbitonasal fenestra. It supplies blood to the posteromedial portion of the paraseptal cartilage of the nasal capsule. In modern iguanid lizards, it pierces the vomer anteriorly (Oelrich, 1956).

In *Eocaptorhinus* there is no direct evidence for the presence of a medial ramus of the inferior nasal artery although the large medial orbitonasal fenestra could easily have accommodated it. If the medial ramus of the inferior nasal artery did exist in *Eocaptorhinus*, it did not penetrate the vomer as it does in iguanid lizards.

Arteria nasalis inferior ramus lateralis (ANL)

The lateral ramus of the inferior nasal artery of lizards descends vertically until it contacts the dorsal surface of the palatine immediately posterior to the orbitonasal ridge and membrane. Here it turns laterally to run in a deep groove between the orbitonasal and periorbital membranes (Oelrich, 1956). The lateral ramus enters the lateral nasal fenestra with the intermediate palatine nerve and the lateral palatine artery. Both the lateral ramus of the inferior nasal artery and the intermediate palatine nerve immediately enter the posterior palatine canal of *Eocaptorhinus* which, unlike that of lizards, bifircates and opens through two anterior palatine foramina within the posteroventral margin of the internal naris. It is not known whether these foramina carried the nerve and artery separately or whether one or both divided within the canal to send both arterial and nerve branches from each foramen. It is probable that both of the anterior palatine foramina carried arterial branches in order to supplement the otherwise meagre supply of blood to the ventral surface of the palate to judge by the small size of the suborbital fenestra. The lateral ramus of the inferior nasal artery presumably supplied the oral mucosa and the incisive pad lining the anterior portion of the ventral surface of the palate and the choanal epithelium within the posterolateral part of the internal naris as in modern lizards.

Arteria orbitalis inferior (AOI)

The inferior orbital (infraorbital) artery is found in all reptiles. In *Sphenodon*, lizards, crocodilians, and primitive turtles the inferior orbital artery arises as a ventral branch of the temporal artery (Rathke, 1863; Shindo, 1914; O'Donoghue, 1920; Oelrich, 1956). In advanced turtles including the kinosternid and trionychid cryptodires, a secondary origin of the inferior orbital artery has developed from the palatine artery (McDowell, 1961; Albrecht, 1967). The inferior orbital artery descends along the posterior surface of the orbitotemporal membrane to where it meets the mandibular ramus of the trigeminal nerve. Together they continue ventrally to pass beneath the periorbital membrane where they cross the dorsal surface of the pterygoid and palatine to the anterolateral corner of the orbit. Here they extend along a prominent groove between the anterior process of the jugal and the palatine in line with the conjunctival groove when present (in *Sphenodon* and lizards only). Where the inferior orbital artery crosses the floor of the orbit it produces a small anterior orbital artery (AOA). The inferior orbital artery, accompanied by the maxillary nerve continues forward in the conjunctival groove until they both reach the infraorbital foramen at which point they are joined by the lateral palatine nerve which forms a ganglionic union with the maxillary nerve before the artery and the united nerves enter the infraorbital foramen (Bojanus, 1819-21; Watkinson, 1906; Oelrich, 1956).

The inferior orbital artery of *Eocaptorhinus* (Figs. 5, 6, and 9) appears to have followed the same path as it does in modern *Sphenodon*, lizards, crocodilians, and many turtles. As in *Sphenodon* and lizards, *Eocaptorhinus* has a deep conjunctival groove in line with the infraorbital foramen. Presumably the inferior orbital artery, accompanied by the maxillary nerve, entered the infraorbital foramen, where it became the maxillary artery, probably anterior to a final ganglionic connection between the maxillary and lateral palatine nerves. Just before entering the infraorbital foramen the inferior orbital artery produced the anterior orbital artery.

Arteria orbitalis anterior (AOA)

An anterior orbital artery is present in lizards (Oelrich, 1956) and in turtles where it is often referred to as the alveolar-nasal artery (Albrecht, 1967). It is much smaller than the inferior orbital artery. In *Sphenodon* no anterior orbital artery has been described although such a reported absence should be regarded with suspicion. The anterior orbital artery supplies blood to the anterior corner of the orbit and then extends anteriorly along the medial side of the lachrymal duct which in lizards is

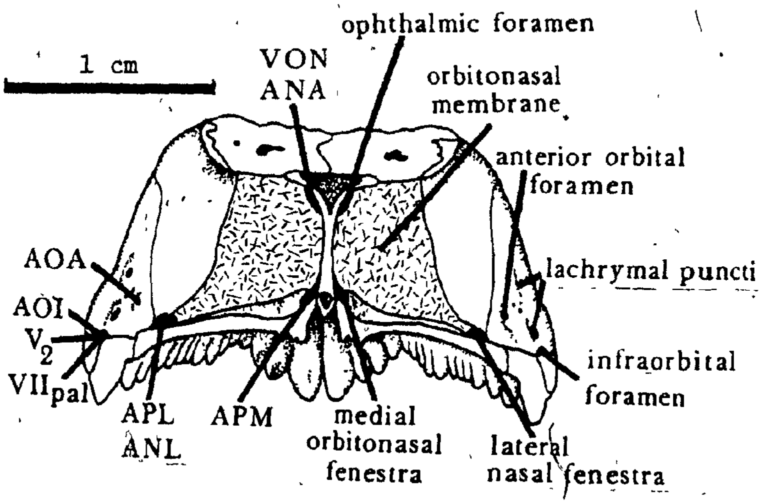


Figure 9. *Eocaptorhinus laticeps*. Anterior portion of orbit in posterior aspect showing orbitotemporal membrane, foramina, and nerves and blood vessels believed to pass through the foramina. Reconstruction.

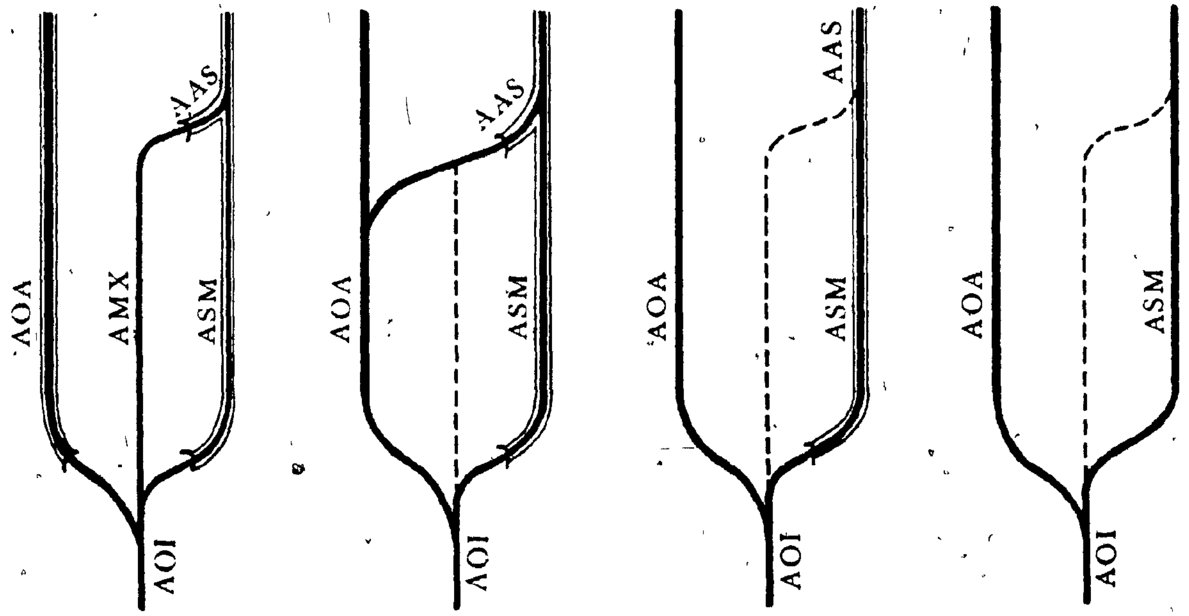
not enclosed in a bony canal (Oelrich, 1956). In turtles where there is no lachrymal duct, the anterior orbital (postnarial) artery supplies the posterior region of the nasal capsule before entering the medial superior alveolar foramen. The circulatory system of the orbit in crocodilians is not known in detail so that the presence of an anterior orbital artery is unknown.

Eocaptorhinus is thought to have possessed a well developed anterior orbital artery. The lachrymal duct was completely enclosed within an osseous lachrymal canal in contrast to modern lizards. The anterior orbital artery is believed to have entered the bone through the anterior orbital foramen that is situated just medial to the conjunctival groove and midway between the two large lachrymal puncti. The artery would have passed through the short anterior orbital canal to emerge on the medial side of the lachrymal duct at the confluence of the lachrymal puncti. Fine pores that are situated at the bases of the sculpture pits may have served for the passage of branches of the anterior orbital artery through the vesicular bone of the lachrymal to supply the skin. Five tiny foramina that are aligned horizontally along the medial wall of the lachrymal above the lachrymal ridge (Fig. 8) may have accommodated other fine arterioles which may have supplied blood to a lateral nasal gland.

Arteria maxillaris (AMX)

The divisions of the inferior orbital artery are quite varied in form in modern reptiles depending upon the type of tooth implantation (or lack of teeth) as well as upon the presence or absence of a secondary palate. All modern reptiles are probably specialized from the primitive pattern. Basically there are three branches of the maxillary artery, two intraosseous and one extraosseous. The supramaxillary artery (ASM) lies within the supramaxillary (infraorbital) canal and the superior alveolar artery (ASA) within the superior alveolar canal. The maxillary artery lies medial to the maxilla lateral to the nasal casule and is not enclosed within a bony canal. Turtles appear to have the least specialized pattern of inferior orbital artery divisions for they have retained the superior alveolar and supramaxillary canals and associated arteries (Fig. 10). The reduction and subsequent disappearance of the osseous lachrymal canal brought the anterior orbital (alverolar-nasal) artery into close contact with the maxillary artery, with the latter eventually being lost and the superior alveolar artery forming a connection with the anterior orbital artery (Fig. 10). This connection is not present in either *Sphenodon* or lizards. In *Sphenodon* and acrodont lizards (agamids, chamaeleonids), a supramaxillary canal is present that carries a single supramaxillary (and confluent superior alveolar) artery that has usually been referred to as the maxillary artery (O'Donoghue, 1920). This artery nourishes the free margin of the dental lamina of the maxillary teeth. In pleurodont lizards where the primitive superior alveolar supramaxillary canals have been lost, only one extraosseous artery is present. This is usually termed the maxillary artery (Oelrich, 1956). Its main function is to supply blood to the free margin of the dental lamina of the maxillary teeth just as does the supramaxillary artery of *Sphenodon*. The extensive modificiation of the maxilla inherent in the development of the crocodilian secondary palate and pneumatization makes interpretation of the inferior orbital artery division pattern of this group difficult.

As in turtles, *Eocaptorhinus* has a long supramaxillary canal extending anteriorly from the supramaxillary foramen to where it meets the small



Eocaptorhinus Turtle *Sphenodon* Pleurodont Lizard

Figure 10. Schematic representation of the branches of the inferior orbital artery entering the snout in *Eocaptorhinus*, in a turtle in *Sphenodon* and acrodont lizards, and in pleurodont lizards.

medial superior alveolar canal and, thence, continues further anteriorly as the superior alveolar canal. The supramaxillary artery presumably extended anteriorly through the supramaxillary canal until it joined the superior alveolar artery (Fig. 8). Unlike turtles, however, there was no connection between the anterior orbital artery and the superior nasal artery since the lachrymal duct and the closely associated anterior orbital artery were presumably enclosed in a heavy osseous canal that had no known connection with the medial superior alveolar canal. It is probable that a superior alveolar artery was present that would have been supplied by an extraosseous maxillary artery. Where the inferior orbital artery of *Eocaptorhinus* passed through the infraorbital foramen, it apparently bifurcated, sending the supramaxillary artery laterally into the supramaxillary foramen and the maxillary artery medially into the narial chamber. A prominent groove along the medial surface of the maxilla joining the superior alveolar foramen and the supramaxillary foramen and lying just dorsal to the suture between the maxilla and the palatine is believed to have carried the maxillary artery (Fig. 8). This artery does not have a homologue in modern turtles, *Sphenodon,* or acrodont lizards. The maxillary artery of pleurodont lizards appears, at least in part, to be homologous with that thought to have existed in *Eocaptorhinus*. The crocodilian pattern is not known.

It is apparent from the structure of the maxilla that the maxillary artery of *Eocaptorhinus* produced at least one anterior branch, the subnarial artery (ASN) and probably a postnarial artery (APN) as well. In pleurodont lizards, these branches form from what is usually termed the superior alveolar artery (Oelrich, 1956). It is apparent that the superior alveolar artery of pleurodont lizards is not homologous with the similarly named artery in turtles or in *Eocaptorhinus* and may, in fact, be homologous with the anterior portion of the maxillary artery that was apparently present in *Eocaptorhinus*.

Arteria supramaxillaris (ASM)

The supramaxillary artery is a lateral branch of the inferior orbital artery that enters the supramaxillary foramen and extends through the supramaxillary canal (Figs. 8 and 10). It is well formed in turtles (Albrecht, 1967) and in *Sphenodon* where it has been called the maxillary artery (O'Donoghue, 1920). Acrodont lizards also have a supramaxillary artery that, as in *Sphenodon*, supplies blood to the free margin of the dental lamina and to the teeth. Similarly, the posteroventral expanse of the triturating surface of turtles is supplied by the supramaxillary artery. In turtles the supramaxillary artery anastomoses with the superior alveolar artery anteriorly.

In pleurodont lizards there is no supramaxillary canal, nor is there a supramaxillary artery. The single artery running along the medial surface of the maxilla is termed the maxillary artery since it is extraosseous in form but its function, to supply blood to the dental lamina and teeth, is more like that of the supramaxillary artery. If, as the structure of *Eocaptorhinus* intimates, both an extraosseous maxillary artery and an intraosseous supramaxillary artery were present primitively then, with the reduction of ossification of the maxilla in pleurodont lizards, one of these arteries was lost but which is not certain. It appears that the supramaxillary artery became reduced and eventually was lost and that the maxillary artery was retained in modified form to supply blood to the teeth and dental lamina.

The supramaxillary artery of *Eocaptorhinus* appears to have been identical to that of turtles, having entered the supramaxillary canal through the supramaxillary foramen and extended anteriorly to join the superior alveolar artery. The supramaxillary artery supplied the dental lamina and pulp cavities of the post-caniniform teeth. In addition, fine arterioles passed laterally through fine pores in the sculpture pits of the maxilla to supply the skin and external "lips". There were no mental foramina as in procolophonids, rhynchocephalians, or lizards through which branches of the supramaxillary artery could reach the skin.

Arteria alveolaris superior (AAS)

In turtles a well developed lateral extension of the anterior orbital (alveolar-nasal) artery enters the medial superior alveolar canal through the superior alveolar foramen. It continues laterally until it enters the main portion of the superior alveolar canal where it anastomoses with the supramaxillary artery (Fig. 10). In *Eocaptorhinus* the anterior orbital artery was apparently enclosed within the osseous lachrymal canal and so did not join the superior laveolar artery. Blood was supplied to it by the extraosseous mandibular artery. Otherwise, the superior alveolar artery of *Eocaptorhinus* appears to have been identical in form to that of turtles. It supplied blood to the dental lamina and pulp cavities of the caniniform and pre-caniniform teeth.

A superior alveolar artery has been described in lizards as a continuation of the maxillary artery that extends anteriorly through the superior alveolar canal to produce two important branches, the postnarial artery and the subnarial artery. It appears likely that the superior alveolar canal and artery of lizards is not homologous with that of turtles or, apparently, of *Eocaptorhinus*. In turtles and *Eocaptorhinus* the superior alveolar canal does not open anteriorly into the external naris, thereby preventing the formation of postnarial and subnarial arteries from the superior alveolar artery in both of these forms. In conjunction with the loss of the septomaxilla in turtles, neither the postnarial nor the subnarial artery has developed, at least in recognizable form. This appears to be a specialized condition, for the primitive form, *Eocaptorhinus*, evidently had both a postnarial and subnarial artery that developed as an anterior extension of the maxillary artery. In *Eocaptorhinus*, a prominent groove separating the main body of the maxilla laterally from the septomaxillary tubercle medially may have served for the passage of the maxillary-subnarial artery. It is believed that the primitive superior alveolar canal degenerated in pleurodont lizards concommitantly with the supramaxillary canal, this leading to the associated reduction and eventual loss of the superior alveolar and supramaxillary arteries and the assumption of their functions by the maxillary artery. If this is true it is probable that the superior alveolar canal of pleurodont lizards is a neomorph developed from the groove separating the main body of the maxilla from the septomaxillary tubercle by increased vertical growth of the septomaxillary tubercle and dorsal fusion with the high maxilla. This is given considerable support by the fact that in primitive lizards (iguanids and gekkos) the superior alveolar canal, perhaps more correctly termed the anterior maxillary canal, is much shorter than in more advanced lizards (varanids). It is believed that there is a correlation between the development of the anterior maxillary canal in lizards and the increase in height of the maxilla and reduction in size of the lachrymal.

Arteria postnarialis (APN)

A well developed postnarial artery is known in lizards (Oelrich, 1956) branching dorsally from the maxillary artery upon leaving the anterior maxillary canal and supplying blood to the posterior region of the vestibule of the nasal capsule immediately posterior to the septomaxilla. A postnarial artery has not been reported in either turtles or crocodilians, where the septomaxilla has been lost, or in *Sphenodon*. It is possible that the lack of reference to such an artery is a result of the lack of detailed study of the arterial supply to the snout in these animals.

The apparent similarity between the development of the anterior maxillary canal in lizards and the groove lateral to the septomaxillary tubercle in *Eocaptorhinus* suggests that blood was supplied to the posterior region of the vestibule of the nasal capsule by a lizard-like postnarial artery. In turtles the vestibular region of the nasal capsule is supplied through the anterior orbital (alveolar-nasal) artery (Albrecht, 1967). It is not known how this region is supplied in crocodilians where the extreme modification inherent in the development of the secondary palate has obscured many of the relationships between the soft anatomy and bones of the skull.

Arteria subnarialis (ASN)

In pleurodont lizards, a fine extension of the maxillary artery passes anteriorly over the premaxillary process of the maxilla, lateral to the septomaxilla, ventral to the vestibule of the nasal capsule. It continues around the internal surface of the premaxilla to send a tiny branch through the prepalatal foramen of the premaxilla to anastomose on the ventral surface of the vomer and to supply blood to the fleshy incisive pad (Oelrich, 1956). In *Sphenodon* an anterior continuation of the superior alveolar artery exists from the lateral surface of the maxilla then extends forward below the external naris (O'Donoghue, 1920). It does not appear to enter the snout anterior to the vestibule of the nasal capsule. Blood is supplied to the vestibular region by ventral branches of the nasal artery.

In turtles there appears to be no subnarial artery. The prepalatal foramen of turtles does not transmit a subnarial artery. A subnarial artery is present in crocodilians but its homologies are not fully understood.

In *Eocaptorhinus* there is, as in lizards, a well developed prepalatal foramen anterior to the typical turtle position, as well as a large posterior premaxillary foramen. It is believed that a lizard-like subnarial artery entered the snout and sent branches through each foramen, the former to supply the vomerine raphe with blood and the latter to nourish the teeth and dental lamina of the premaxilla.

Arteria mandibularis (AMN)

The mandibular artery of modern lizards and *Sphenodon* is formed as a prominent proximal branch of the stapedial artery that turns laterally and then ventrally (Shindo, 1914; O'Donoghue, 1920; Oelrich, 1956) to pass between the M. adductor mandibulae externus laterally and the M. adductor mandibulae posterior and M. adductor mandibulae internus (M. pseudotemporalis) medially (Oelrich, 1956; Haas, 1973). Just before entering the adductor fossa it produces a number of smaller arteries to the muscles and, at least in lizards, and anterior and posterior condylar artery. As the mandibular artery reaches the dorsal edge of the lower jaw it divides into an internal and an external mandibular artery (AMI and AME, respectively).

Some turtles such as *Testudo* retain a primitive origin of the mandibular artery from the stapedial artery. In many other turtles

(Emys, Kinosternon, Trionyx) the extensive remodelling of the braincase has led to the reduction and loss of the proximal portion of the mandibular artery. In these forms, the mandibular artery originates as a ventral extension of the inferior orbital artery (Bojanus, 1819-21; Shindo, 1914). Crocodilians exhibit a highly modified braincase that may be related to the loss of the proximal portion of the mandibular artery. A secondary anastomosis of the external carotid has occurred with both the inferior orbital and mandibular arteries. Neither turtles nor crocodilians have external mandibular arteries (Bojanus, 1819-21; Shindo, 1914).

Since the braincase of *Eocaptorhinus* is primitive with communication between the adductor chamber and the middle ear cavity, it is probable that the mandibular artery originated from the stapedial artery as in *Sphenodon*, lizards, snakes, and some turtles (e.g.*Testudo*). Because of the low position of the quadrate ramus of the pterygoid relative to the articular surface of the quadrate, it is unlikely that a posterior condylar artery extended posteriorly from the mandibular artery beneath the pterygoid. Whether the mandibular artery divided is not known although there is no evidence that there was an external mandibular artery.

Arteria mandibular interna (AMI)

Just before entering the adductor fossa, the mandibular artery in *Sphenodon* and lizards divides. The internal branch runs anteriorly along the dorsal surface of the Meckelian cartilage where it produces several medial intermandibular branches. It anastomoses laterally with the external mandibular artery through the mental foramina. The anterior extremity of the internal mandibular artery reaches the "chin" through the symphysis as the symphysial artery (ASY). The internal mandibular artery of turtles and crocodilians is similar except that, in the absence of an external mandibular artery, there is no lateral anastomosis and hence no mental foramina. In *Eocaptorhinus* an internal mandibular artery appears to have been present in the typical reptilian position giving rise to several intermandibular arteries and a terminal symphysial artery.

Arteria intermandibularis caudalis (AIC)

Amongst modern retpiles, only crocodilians have a large foramen intermandibularis caudalis (Mecklian foramen) similar to that of *Eocaptorhinus*. In *Sphenodon* where the splenial has been lost, there are no separate foramina, only a long sulcus. In turtles and lizards, the foramen intermandibularis caudalis is greatly reduced yet always retained. In all modern reptiles, the intermandibularis caudalis artery, a branch of the internal mandibular artery, accompanied the ramus intermandibularis caudalis of the mandibular division of the trigeminal nerve (V_3) to nourish the M. geniohyoideus. It is believed that a similar arrangement occurred in *Eocaptorhinus*.

Arteria intermandibularis medius (AIM)

A tiny foramen intermandibularis medius is present in lizards and crocodilians. In turtles and *Sphenodon* the foramen lies within the sulcus cartilaginis meckelii (Gaffney, 1972). In *Eocaptorhinus* two extremely small chevron-shaped canals about 2 mm long extend dorsally between the dentary and splenial, appear to represent the foramen (foramina) intermandibularis medius, thus conforming in position to the pattern seen in lizards. In modern reptiles the intermandibularis medius branch of the internal mandibular artery passes through this foramen accompanied by the ramus intermandibularis medius of the mandibular division of the trigeminal nerve

(V_3) and the ramus chorda tympani of the facial nerve (VII_{cht}). In pleurodont lizards, blood is supplied to the dental lamina of the teeth by this artery. In all modern reptiles blood and nerve endings to to the gustatory and mucosal tissue of the inner "lips". Two small foramina in *Eocaptorhinus* appear to have carried the same nerves and the intermandibularis artery as in modern reptiles, possibly with the nerves extending through one canal and the artery through the other.

Arteria intermandibularis oralis (AIO)

In lizards and crocodilians there is a small foramen intermandibularis oralis within the splenial while in *Sphenodon* and turtles this foramen lay within the sulcus cartilaginis meckelii (Gaffney, 1972). In *Eocaptorhinus* a prominent foramen intermandibularis oralis is found within the splenial. It appears that, as in modern reptiles, the intermandibularis oralis artery and nerve passed through this foramen to nourish and innervate the origins of the M. genioglossus anteriorly and the M. intermandibularis oralis posterorly.

Arteria symphysialis (ASY)

A symphysial artery extending anteriorly from the internal mandibular artery below the symphasis of the two mandibular rami to nourish the skin of the "chin" is found in lizards and crocodilians. In turtles, where this region is covered by a heavy keratinous beak, there is no symphysial artery. The skin covering the "chin" in *Sphenodon* is nourished by the external mandibular artery.

In *Eocaptorhinus* a well developed canal passes anteriorly through the symphysis and is believed to have carried a symphysial artery.

Arteria alveolaris inferior (AAI)

Sphenodon, lizards, and turtles among modern reptiles have an inferior alveolar artery that branches laterally from the internal mandibular artery within the adductor fossa and enters the inferior alveolar canal through the inferior alveolar foramen. In *Sphenodon* this artery supplies blood to the teeth and dental lamina of this acrodont form, while in edentulous turtles the artery supplies blood to the triturating surface of the dentary. This system has not been reported in either crocodilians of lizards although it is to be expected in acrodont (agamid, chamaeleonid) lizards. Additionally, in *Sphenodon* and lizards, cutaneous branches extend laterally through the mental foramina.

In *Eocaptorhinus* a prominent inferior alveolar canal and foramen is present although much further anteriorly (posterior extremity at the eighth tooth position) than in either turtles or *Sphenodon*. It is apparent that this canal carried the inferior alveolar artery to the teeth and dental lamina.

Anteria mandibularis externa (AME)

Turtles and crocodilians do not have external mandibular arteries. In the former most of the lateral surface of the dentary is covered by the closely adhering keratinous beak. In the latter, blood is supplied to the skin internally from the internal mandibular artery. In *Sphenodon* and lizards there is a large external mandibular artery that branches laterally from the mandibular artery, passing dorsal to the surangular and posterior to the coronoid, then turning to run anteriorly along the lateral surface of the mandible where it nourishes the skin and anastomoses with the inferior alveolar artery (*Sphenodon* and acrodont lizards) or the internal mandibular artery (pleurodont lizards). In *Sphenodon* a posterodorsal extension of the surangular and an anterodorsal projection of the articular meet above the external mandibular artery to produce the neomorphic articular foramen.

The mandible of *Eocaptorhinus* most closely resembles that of crocodilians with an internal blood supply to the skin. It is, therefore, probable that an external mandibular artery did not exist.

Arteria palatina (APA)

The palatine artery is an anterior continuation of the internal carotid anterior to the separation of the posterior cerebral artery (ACB). In *Sphenodon* and lizards it passes anteriorly through the vidian canal to emerge on the dorsal surface of the pharyngeal membrane and ventral to the inferior orbital membrane. Here is produces a small dorsal muscular ramus that supplies blood to the M. levator pterygoidei and the M. protractor pterygoidei, then continues anteriorly where it divides to produce a large medial palatine artery (APM) and lateral palatine artery (APL).

In turtles, the palatine artery is entirely enclosed within the internal carotid canal. There is no dorsal muscular ramus since the M. levator pterygoidei and M. protractor pterygoidei have been lost. Within the internal carotid canal, the palatine artery of many turtles (e.g. testudinids) divides into a medial palatine artery (palatine artery of McDowell, 1961; Albrecht, 1967). and a lateral palatine artery (posterior vidian artery of Albrecht, 1967).

The palatine artery of crocodiles continues anteriorly through the internal carotid canal to emerge on the dorsal surface of the pterygoid which forms part of the secondary palate. There is no pterygoid artery. It has not been determined whether there is a lateral palatine artery.

There is no vidian or internal carotid canal in *Eocaptorhinus*, rather, there is a deep sulcus on the ventral surface of the basipterygoid process between the basisphenoid and the crista ventrolateralis of the parasphenoid. It is apparent that the palatine artery passed anteriorly through this sulcus before producing a small pterygoideus artery and larger medial and lateral palatine artery (Fig. 4). Pelycosaurs also possess a similar deep vidian sulcus. Amongst the primitive reptilian groups procolophonids and pareiasaurs had developed lepidosaur-like vidian canals. A similar formation of a vidian canal has been demonstrated in a number of labyrinthodonts by Shishkin (1968).

Arteria muscularis levator pterygoidei et protractor pterygoidei (APT)

As the palatine artery leaves the vidian canal in lizards, a small branch, a muscular artery, extends dorsally to supply blood to the M. levator pterygoidei and M. protractor pterygoidei (Oelrich, 1956). In the specimens of *Sphenodon* examined by O'Donoghue (1920), this same artery was present. Whether this muscular artery degenerates in older akinetic individuals where the M. protractor pterygoidei is lost is not known (Ostrom, 1962; Haas, 1973). The M. levator pterygoidei and M. protractor pterygoidei and the associated muscular artery are not present in akinetic turtles or crocodiles.

Eocaptorhinus appears to have had a metakinetic skull (i.e. the braincase could move relative to the skull roof) with a movable basicranial articulation as a juvenile but probably became akinetic as an adult. In relationship to this, it has been interpreted that an M. levator pterygoidei and probably an M. protractor pterygoidei were present. A small muscular artery is believed to have curved dorsally around the anterior end of the basisphenoid in a narrow, but deep groove between the basipterygoid tubercle and the cultriform process of the parasphenoid, much as in lizards.

Arteria palatina medialis (APM)

The medial palatine artery is the anterior continuation of the palatine artery. In *Sphenodon* and lizards it traverses the dorsal surface of the pharyngeal membrane along the medial rim of the interpterygoid vacuity and then extends along the dorsomedial surface of the pterygoid (O'Donoghue, 1920; Oelrich, 1956). It does not enter the nasal capsule. Fine arterioles anastomose with those of the lateral palatine artery to supply the inferior orbital membrane. In turtles the medial palatine artery continues anteriorly through the lateral carotid foramen upon the dorsal surface of the pterygoid and the palatine (Albrecht, 1967; Gaffney, 1972). The course of the medial palatine artery is not known in crocodilians.

The medial palatine artery of *Eocaptorhinus* is believed to have been much like that of lizards, passing anteriorly over the dorsal surface of the pterygoid, lateral to the medial ridge. It is unlikely that it entered the nasal capsule since this artery does not do so in modern reptiles. A lateral arteriole anastomosis with the lateral palatine artery is probable.

Arteria palatina lateralis (APL)

The lateral palatine artery of *Sphenodon* and lizards extends from its origin from the palatine artery anterolaterally across the pterygoid immediately anterior to the epipterygoid and the attachment of the orbitotemporal membrane. Just medial to the suborbital fenestra, a short inferior palatal artery is produced. The lateral palatine artery continues anteriorly along the lateral margin of the dorsal surface of the palate, beneath the inferior orbital membrane, to pass through the lateral nasal fenestra into the nasal capsule. A system of arterioles anastomoses medially with branches of the medial palatine artery.

The situation in turtles is extremely variable. Where a lateral palatine (anterior vidian) artery is present as in testudinoids, it resembles the proximal portion in lizards except that it lies within the anterior vidian canal. When present, it does not extend as far anteriorly as the posterior rim of the orbit. In some turtles, such as the trionychids, the lateral palatine artery has been lost completely. This artery has not been described in crocodilians.

The lateral palatine artery of *Eocaptorhinus* is interpreted as having been similar to that of *Sphenodon* and lizards in its course (Fig. 5). It appears to have run anterolaterally through a shallow groove on the heavy medial surface of the neck of the pterygoid immediately anterior to the epipterygoid recess. It passed laterally across the dorsal surface of the pterygoid and palatine anterior to the ridge for the attachment of the orbitotemporal membrane. Although there is no groove identifying the precise course of this artery, its position can be reconstructed with reasonable assurance since the point at which the inferior palatal artery branched laterally into the inferior orbital fenestra is easily determined. It is thought that the lateral palatal artery continued anteriorly to enter the nasal capsule through the lateral palatal fenestra.

Arteria palatina inferioris (API)

In *Sphenodon* and lizards a small lateral branch of the lateral palatine artery, the inferior palatine artery, that accompanies a terminal branch of the lateral palatal ramus of the facial nerve, passes through the inferior orbital fenestra, as does the pterygoid vein, to nourish the oral mucosa lining the ventral surface of the palate. In turtles the same function is performed by the inframaxillary artery, a branch of the inferior orbital artery that passes through the posterior palatine fenestra (Albrecht, 1967). It is not known how the turtle pattern developed or whether the diapsid inferior orbital fenestra is homologous with the chelonian posterior palatine fenestra. The crocodilian palatal arteries have not been described.

A fine inferior palatal artery is believed to have accompanied a branch of the palatine ramus of the facial nerve through the tiny suborbital fenestra in *Eocaptorhinus*. The small size of the fenestra precludes the passage through it of a pterygoid vein as in modern forms.

Since a suborbital fenestra was not present in any pelycosaur, there was no inferior palatine artery. The ventral surface of the palate appears to have been supplied with blood from some other source, most probably the external carotid.

Arteria cerebralis (ACB)

At the point where the palatine artery separates from the internal carotid, in *Sphenodon* and lizards, and enters the vidian foramen, a small dorsal cerebral artery is produced. It enters the posterior internal carotid foramen and internal carotid canal where it bifurcates to produce an anterior cranial ramus and posterior caudal ramus that leave the anterior carotid foramina. In *Eocaptorhinus*, as revealed by the course of the internal carotid canal through the basisphenoid, the pattern appears identical. Extreme modification of the braincase in turtles and crocodilians has altered the form of the internal carotid canals significantly thus obscuring the relationships between the cerebral artery and the skull.

Cranial Venous System

The principal works on the cranial venous system of reptiles are those of Bojanus (1819-21), Corti (1947), Grosser and Brezina (1895), Bruner (1907), and O'Donoghue (1920). No comprehensive study of the cranial venous system of primitive reptiles has ever been undertaken although brief mention has been made by Price (1935) of the position of veins running around or through the braincase of *Captorhinus*. It is only with great difficulty that the venous system of fossil reptiles can be traced. Unlike arteries, which are compact in form and often are held in prominent grooves or canals, veins tend to be more widely dispersed as anastomotic networks or broad sinuses that lie on flat or only slightly depressed bone surfaces. As a result, many of the determinations of size, position, and form of the venous system are based subjectively on spacial relationships and functional interpretations.

The precaval venous systems of most non-mammalian tetrapods are generally similar. The same pattern is assumed to have been present in *Eocaptorhinus* and is the basic form from which the cranial venous system, as described here, was developed. Deoxygenated blood from the head is transported posteriorly through a large common jugular vein or vena jugularis communis (VJC) and from the throat through a vena oesophagea (VOE) to where these veins and the subclavian vein or vena subclavia (VSC) meet to enter the vena cava anterior. The venae cavae anteriores from each side of the head enter the sinus venosus, along with the vena cava posterior. In modern reptiles, the left vena cava anterior is slightly to significantly larger than the right.

Vena jugularis communis (VJC)

Bojanus (1819-21) was the first to describe and illustrate the reptilian vena jugularis communis (truncus venae jugularis) in *Emys orbicularis ("Testudo europaea")*. It is essentially the same as that of *Sphenodon* (termed vena jugularis interna by O'Donoghue, 1920) and lizards (Bruner, 1907). The vena jugularis communis of modern reptiles is a large vein that is formed by the confluence of the vena capitis lateralis (VCL) and the vena mandibularis (VMD) (Figs. 11 and 12). Blood is conducted posteriorly from these veins and from the combined dorsal vena occipitalis (VOC) and vena cerebralis posterior (VCP), which enters the vena jugularis communis dorsally just posterior to the head, into the vena cava anterior. Since this pattern is common to all modern reptiles, except snakes which have developed an additional connection between the maxillary vein and the vena jugularis communis, it is reasonable to expect that the vena jugularis communis was essentially similar in *Eocaptorhinus*.

Vena capitis lateralis (VCL)

Grosser and Brezina (1895) noted, in the early embryonic stages of lizard development, that the primitive vena cardinalis passed ventral to the cranial nerve trunks, while in later embryonic stages, a new vein develops above the post-trigeminal nerve trunks (except the vagus accessory) and the earlier subneural, post-trigeminal segment degenerates. They called this neomorphic supraneural vein the vena capitis lateralis (VCL). Bruner (1907) preferred to group both the vena cardinalis and the post-trigeminal neomorphic vena capitis lateralis together as the vena jugularis interna. This is considered to be inappropriate since it does not correspond to the vena jugularis interna of mammals which is, for the most part, homologous

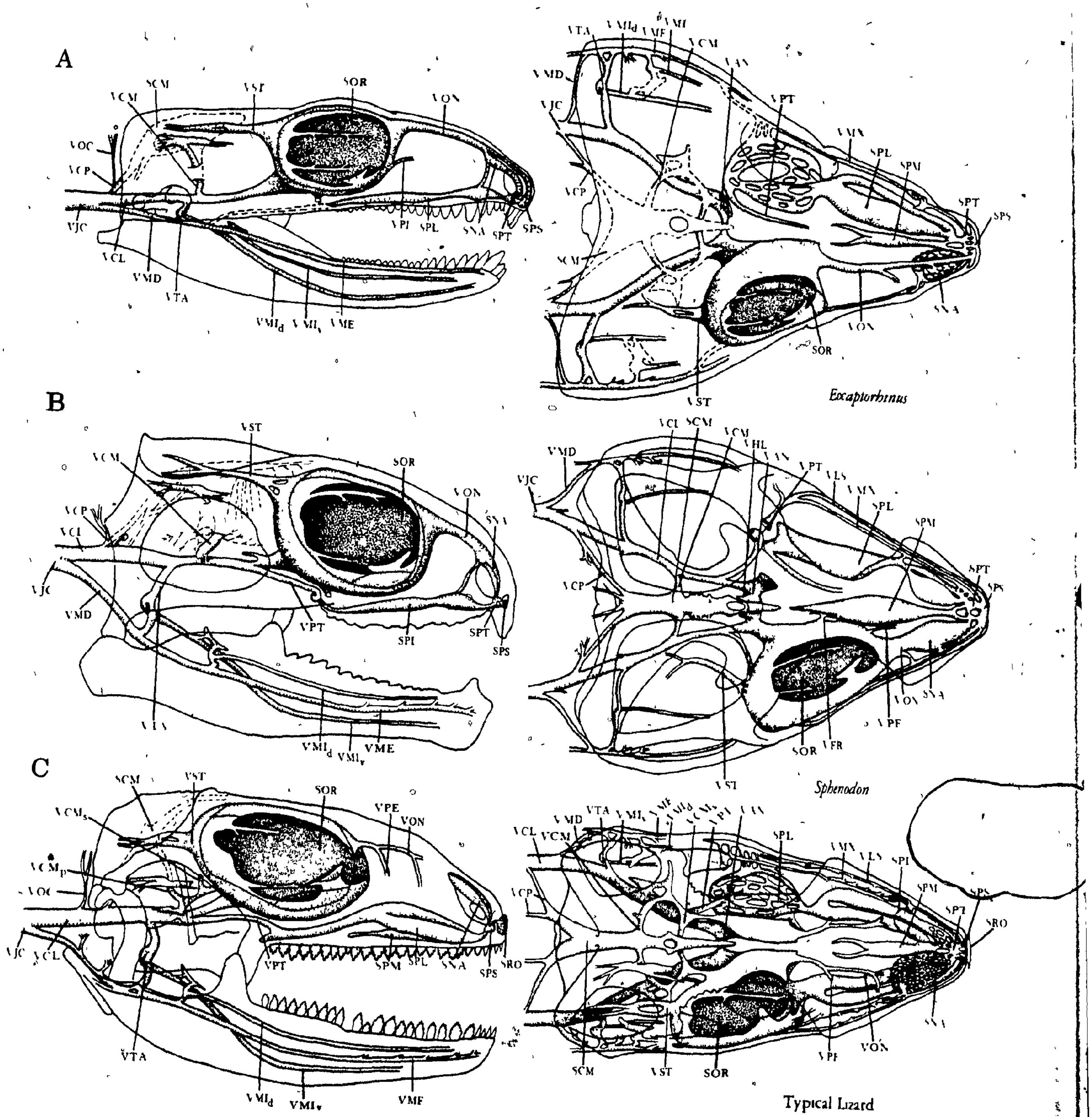
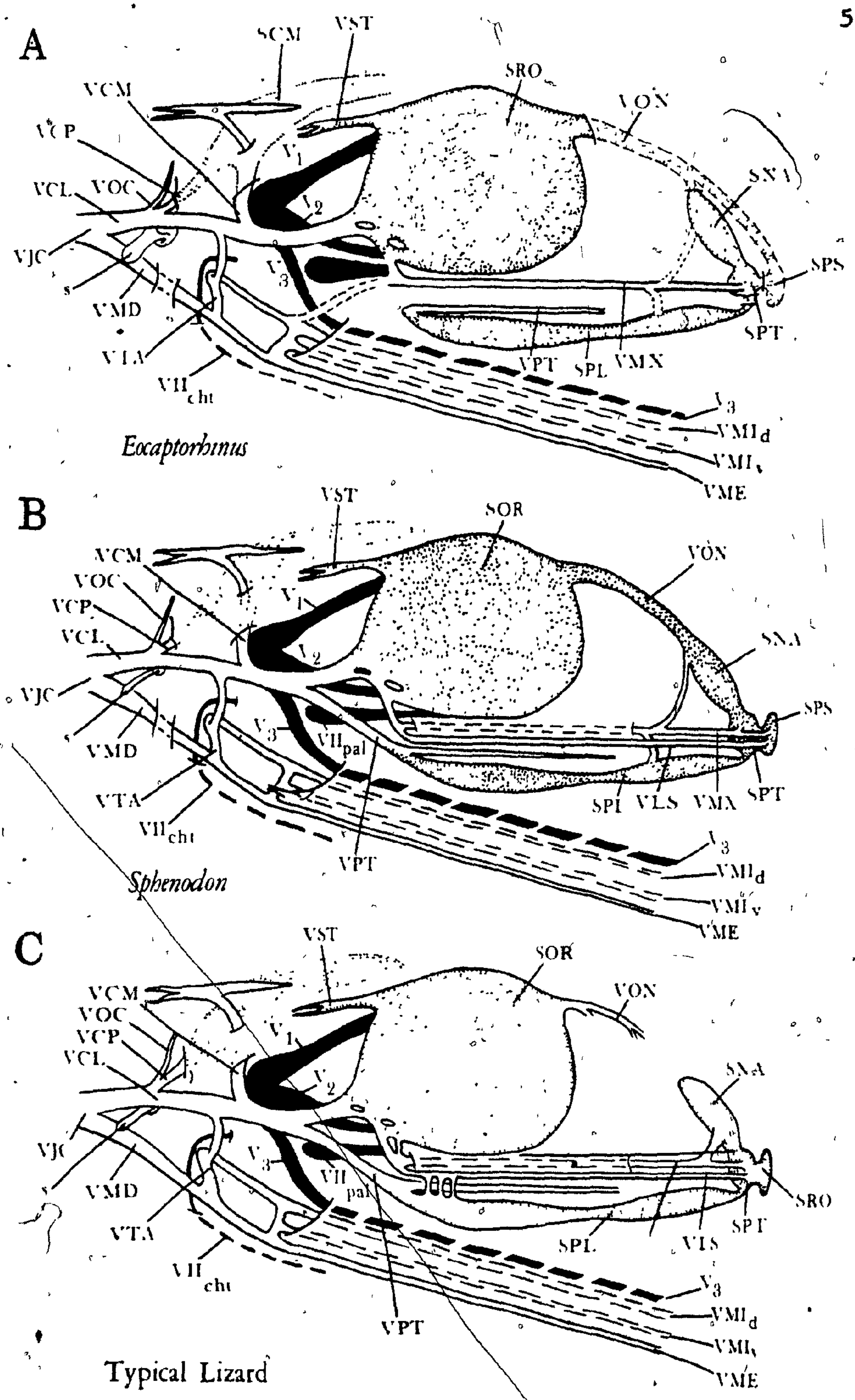


Figure 11. Reconstruction of the venous systems in dorsal and lateral aspect of *Eocaptorhinus*, *Sphenodon*, and a typical lizard (*Iguana* outline representative).



Eocaptorhinus

Sphenodon

Typical Lizard

Figure 12. Schematic reconstruction of major veins in *Eocaptorhinus*, *Sphenodon*, and a typical lizard.

with the vena cerebralis posterior (in part) of *Sphenodon*. Since the original literature is so confused in the establishment of homologies and consequent lack of stability of names, it is deemed preferable to follow Romer's (1956) example of referring to the entire adult vein joining the orbital sinus to the vena jugularis communis, and composed of Grosser and Brezina's (1895) vena cardinalis anterior and vana capitis lateralis (sensu stricto), as the vena capitis lateralis (sensu lato) or lateral head vein. This is by no means the perfect solution but it does avoid the necessity of introducing yet another name into the literature. The vena capitis lateralis (s.l.) of *Sphenodon* has a similar relationship to the cranial nerves as that seen in lizards.

In *Sphenodon* and lizards, the vena capitis lateralis (s.l.) originates from the posteroventromedial corner of the orbital sinus at a point lateral to the subiculum infundibulum of the chondrocranium (Gaupp, 1900; Bruner, 1907) (Figs. 11 and 13). Just posterior to the subiculum infundibulum and anterior to the cristae trabeculares, the left and right venae capitis laterales are joined by a supratrabecular vena anastomotica (VAN) (Bruner, 1907; O'Donoghue, 1920; Save-Soderburgh, 1946). The vena capitis lateralis (s.l.) extends posteriorly dorsal to the basipterygoid processes and along the lateral surface of the braincase, where it receives the pterygoid vein medial to the epipterygoid. As it passes ventral to the Gasserian ganglion, the vena capitis lateralis (s.l.) receives one dorsal vein in *Sphenodon* and amphisbaenids or two in other (non-amphisbaenid) lizards. The latter have a neomorphic vena cerebralis media secunda that enters the dorsal side of the vena capitis lateralis (s.l.) anterior to the maxillary division of the trigeminal nerve. In all lepidosaurs a primitive vena cerebralis media (*Sphenodon* and amphisbaenids) or vena cerebralis media prima (non-amphisbaenid

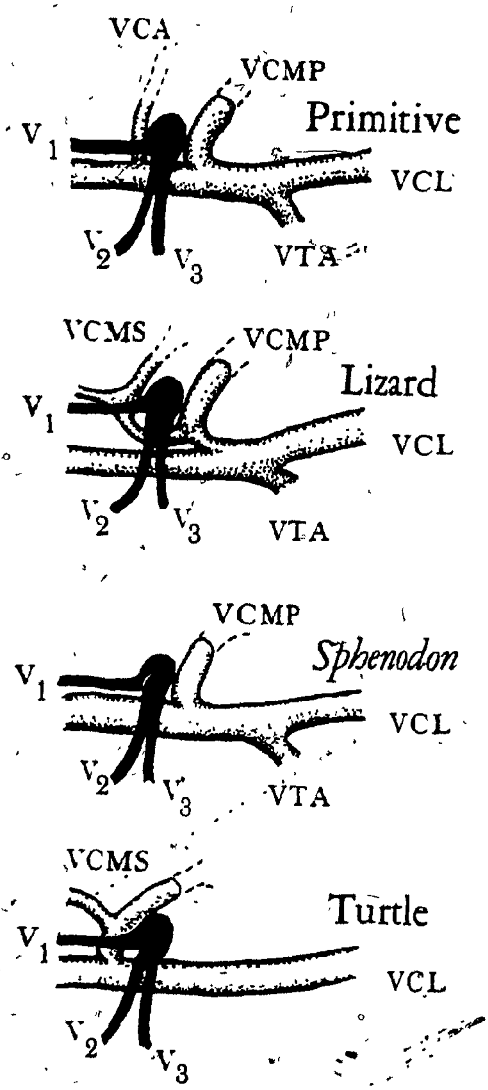


Figure 13. Vena capitis lateralis of a primitive reptile (reconstructed) and of a modern lizard (except amphisbaenids), *Sphenodon* and amphisbaenid lizards, and a turtle.

lizards) joins the vena capitis lateralis (s.l.) dorsally just posterior to the mandibular vein, the vena tympanica anterior (VTA). The course of the vena capitis lateralis (s.l.) receives a ventral anastomotic connection from the mandibular vein, the vena tympanica anterior (VTA). Thus far, the course of the vena capitis lateralis (s.l.) corresponds to the position of the embryonic vena cardinalis anterior (Grosser and Brezina, 1895; Bruner, 1907).

The vena capitis lateralis (s.l.) then curves slightly dorsally above the post-trigeminal cranial nerves (except the vagus accessory nerve). The position of this vein relative to the trunk of the auditory nerve (VIII) cannot be determined but it is generally implied that the vena capitis lateralis (s.l. and s.s.) develops dorsal to it (Grosser and Brezina, 1895; Bruner, 1907). The vena capitis lateralis continues posteriorly dorsal to the stapes (columella auris) and then receives numerous small branches draining the braincase and occipital region including the vena cerebralis posterior (VCP) and the vena occipitalis (VOC) before joining the mandibular vein to form the vena jugularis communis.

Only Bojanus (1819-21) has illustrated the vena capitis lateralis (s.l.) of turtles. This vein which he regarded as a combined sinus cavernosus-vena jugularis extends posteriorly from the orbital sinus (regarded as separate venae ophthalmicae by Bojanus). It is generally similar to the vena capitis lateralis (s.l.) of lepidosaurs, receiving a medial vena anastomotica, vena pterygoidei (vena infraorbitalis of Bojanus) and a large, single, dorsal pre-trigeminal vena cerebralis media (secunda) (Bruner, 1907). Bruner reported that the vena capitis lateralis (s.l.) continues posteriorly below the otic capsule and the auditory nerve thence over the remaining cranial nerves to receive the vena cerebralis posterior then to join the mandibular vein to form the vena jugularis communis. In both *Pseudemys scripta* and *Chelydra serpentina*, the vena capitis lateralis passes through a heavily walled canal (canalis cavernosus) between the braincase and the greatly expanded epipterygoid and quadrate and the highly modified prootic and opisthotic (Gaffney, 1972). Although almost completely enclosed in bone, the vena capitis lateralis (s.l.) is not intracranial (within the braincase) as Grosser and Brezina (1895) reported but extracranial (Gaupp, 1900; Bruner, 1907). Since the auditory nerve is entirely intracranial, it is not certain how Bruner (1907) established that the vena capitis lateralis (s.l.) passed ventral to the auditory nerve in contrast to lepidosaurs where it is above the nerve. In *Pseudemys* and *Chelydra*, the vena capitis lateralis extends lateral to the otic capsule, ventral to the otic capsule, ventral to the membranous labyrinth (semicircular canals), but dorsal to the stapes. This is the same course followed by the vena capitis lateralis of modern lepidosaurs.

In crocodiles and birds, the extensive remodelling of the skull, and especially the braincase, in the course of archosaur evolution, has led to the loss of the vena capitis lateralis (s.l.) and its replacement by a secondary, more laterally position vein (van Gelderen, 1924).

The vena capitis lateralis (s.l.) of *Eocaptorhinus* is believed to have been similar to that of modern non-archosaurian reptiles. It was apparently the largest cranial vein (Figs. 4, 5, and 6) into which drained several intracranial veins, as well as the orbital sinus and possibly one or more extracranial veins. It apparently extended posteriorly along the dorsal surface of the neck of the pterygoid between the orbitotemporal and periorbital membranes. It continued posteriorly along the lateral surface of the braincase, medial to the epipterygoid. The vena capitis lateralis is believed to have passed over the basicranial articulation and then entered a shallow groove on the lateral surface of the basisphenoid that it followed posterior dorsolateral to the vidian (palatine) ramus of the facial nerve until it passed ventral to the paroccipital process, dorsal to the columella of the stapes and medial to the dorsal process (Price, 1935). It is presumed to have passed ventromedial to the foramen through which the hyomandibular ramus of the facial nerve left the braincase. There is a deep groove in the posterior surface of the dorsal process of the stapes of *Eocaptorhinus* that is aligned with the dorsal surface of the columella over which the vena capitis lateralis (s.l.) is believed to have passed. It appears that the hyomandibular ramus of the facial nerve descended across the lateral face of the footplate of the stapes, then passed ventral to the vena capitis lateralis (s.l.), just as in modern reptiles, and then entered the groove on the posterior surface of the dorsal process. Caudad of the stapes, the vena capitis lateralis (s.l.) seemingly turned slightly ventrally to pass beneath the opisthotic to its junction with the mandibular vein to form the vena jugularis communis.

A number of veins are believed to have entered the vena capitis lateralis (s.l.) along its length. Since a vena anastomotica joining right and left venae capitis laterales (s.l.) is present in all modern reptiles, its presence is regarded as virtually assured in *Eocaptorhinus*, probably dorsal to the trabecula communis and just anterior to the prominent cristae trabeculares of the basisphenoid. It is probable that the dorsal surface of the palate ventral to the suborbital membrane and the region of the interpterygoid vacuity was drained by a small medial pterygoid vein, although giving no physical evidence of its presence. It is thought to have entered the vena capitis lateralis (s.l.) laterally, medial to the epipterygoid.

Beneath the trigeminal notch, just anterior to the paroccipital process, the vena capitis lateralis (s.l.) is believed to have received a pretrigeminal vena cerebralis media secunda (VCMS) and a post-trigeminal vena cerebralis media prima (VCMP) just as in non-amphisbaenid lizards (van Gelderen, 1924). Bruner (1907), however, does not show a union of the vena capitis lateralis (s.l.) and the vena cerebralis media secunda in *Lacerta*. This pattern is believed to be primitive since it is present in some fish and in non-therian mammals as well as lizards. Van Gelderen (1924) and Goodrich (1930) believed that only a post-temporal segment was present in "protetrapods". It seems preferable to regard a bipartite vena cerebralis media as the primitive condition as retained by non-amphisbaenid lizards. The single post-trigeminal vena cerebralis media (prima) in *Sphenodon* and amphisbaenids (Grosser and Brezina, 1895; Bruner, 1907; Dendy, 1909; O'Donoghue, 1920) has resulted from the loss of the vena cerebralis media secunda just as in turtles (as far as is known) the vena cerebralis media secunda is retained and the apparently redundant vena cerebralis media prima eliminated (Bojanus, 1819-21; Bruner, 1907). *Eocaptorhinus* is reconstructed (Fig. 6) with both the ramus primus and ramus secundus.

The presence of a vena tympanica in *Eocaptorhinus* is suspected but cannot be proved. It is reconstructed in its presumed position joining the vena capitis lateralis anterior to the stapes (Fig. 6). After having passed posteriorly dorsal to the stapes the vena capitis lateralis (s.l.) is believed to have received a prominent vena cerebralis posterior that drains the posterior region of the braincase through the vagus (jugular) foramen, or the vagus foramen and foramen magnum. At least one additional vein is believed to have drained the occipital musculature into the vena capitis lateralis (s.l.) before the latter joined the vena mandibularis to form the vena jugularis communis.

Vena anastomotica (VAN)

A vena anastomotica is present in *Sphenodon* (O'Donoghue, 1920), lizards (Bruner, 1907), and turtles (Bojanus, 1819-21) in the same position joining the right and left venae capitis laterales dorsal to the trabecula communis, posterior to the pila metoptic (Kunkel, 1912; DeBeer, 1937), the ventral portion of which forms the subiculum infundibulum in *Sphenodon* (Save-Soderbergh, 1946, 1947) and lizards (Gaupp, 1900; Bruner, 1907; Rice, 1920; DeBeer, 1930), and anterior to the pila antotica. It occupies the most ventral portion of the fenestra metoptica anteroventral to the pituitary body. The venae capitis laterales (s.l.) of snakes have been lost with the orbital drainage being assumed by a large lateral maxillary vein, hence the loss of the vena anastomotica in this group. While crocodilians have lost the posterior portion of the vena capitis lateralis (s.s.), it is not known whether the more anterior portion and a vena anastomotica is retained.

In *Sphenodon*, a small vena hypophysialis lateralis is thought to have entered the posterior side of the vena anastomotica from each side of the fused, medial, subhypophysial segment of the metoptic membrane (O'Donoghue, 1920; Save-Soderburgh, 1946, 1947). Bruner (1907) illustrated a vena hypophysialis that drained laterally into the vena cerebralis media secunda and not into the vena anastomotic. In turtles it appears that a major venous plexus drains the entire forebrain region into the vena anastomotica (Bojanus, 1819-21) but this needs to be reviewed.

Since a vena anastomotica of identical form is present in *Sphenodon*, lizards and turtles, it appears likely that *Eocaptorhinus* had a similar structure. This is supported by evidence that a vena hypophysialis lateralis, similar to that of *Sphenodon*, was present.

Vena hypophysialis lateralis (VHL)

In *Sphenodon*, the sella turcica and the enclosed pituitary body is drained anteriorly into the vena anastomotica through a fine vena hypophysialis lateralis (O'Donoghue, 1920; Save-Soderburgh, 1947). This is quite different from the pattern seen in lizards where a small vena hypophysialis drains the sella turcica and pituitary region laterally into the anterior extremity of the vena cerebralis media secunda where that vein is joined by a secondary connection from the orbital sinus (Bruner, 1907) (Fig. 11). The hypophysial drainage is not well known in turtles, the only good illustrations having been produced by Bojanus (1819-21). There is a well developed primitive vena cerebralis anterior, connected posterodorsally to the pre-trigeminal vena cerebralis media (secunda), into which branches from the forebrain drain and which empties anteriorly into the vena anastomotica (Bojanus, 1819-21; Bruner, 1907). Since the presence of a large vena cerebralis anterior is a primitive character preserved in modern fish and amphibians (van Gelderen, 1924), the pattern of hyomandibular drainage present in turtles appears to be the most primitive amongst modern reptiles. The vena hypophysialis lateralis of *Sphenodon* is believed to represent a reduced vena cerebralis anterior that has lost its connection with the vena cerebralis media (secunda) internally and drains anteriorly into the vena anastomotica just as in turtles. The hypophysial vein of lizards appears to be a neomorph. The hypophysial drainage system of crocodiles has not been described in detail.

It is not possible to determine whether the intracranial portion of the vena cerebralis anterior of *Eocaptorhinus* was a large vessel connected to the vena cerebralis media (secunda) as in turtles or if it was a small vena hypophysialis lateralis as in *Sphenodon*. The extracranial portion of this vessel appears to have run anteriorly along the lateral surface of the median raphe of the metoptic membrane beneath the sella turcica, in which the pituitary body sat, to drain into the vena anastomotica. The median raphe was attached to a low, median septum of the basisphenoid and was flanked laterally by a pronounced groove that lay between the septum and the anterior carotid foramina. The vein that appears to have run through this groove is believed to have resembled the extracranial vena hypophysialis lateralis of *Sphenodon*, hence the use of this terminology for the similar vein in *Eocaptorhinus* in the absence of more detailed information on the form of the intracranial extension of this vein.

Vena cerebralis media (VCM)

The form of the vena cerebralis media is quite varied in modern reptiles. The typical lizard pattern in which a small post-trigeminal vena cerebralis media prima (VCM$_p$) and a larger pre-trigeminal vena cerebralis media secunda (VCM$_s$) appears to be more primitive than the single post-trigeminal vena cerebralis media (prima) of *Sphenodon* and amphisbaenids or the pre-trigeminal vena cerebralis media (secunda) of turtles (Bruner, 1907; van Gelderen, 1924). However, the retention of a well developed vena cerebralis anterior with a connection to the vena cerebralis media (secunda) is turtles is probably a retained primitive character. An analysis of the vena cerebralis anterior and media drainage of modern reptiles suggests a possible ancestral pattern of anterior cerebral drainage employing a well developed vena cerebralis anterior joining a biparatite vena cerebralis media. It is possible that *Eocaptorhinus* had this most primitive vena cerebralis media pattern or a more or less modified one. The lack of ossified anterior cranial walls and the consequent absence of diagnostic osteological reflections of the course of the anterior intracranial circulatory system makes it impossible to determine whether a large vena cerebralis anterior existed in *Eocaptorhinus*. That a well developed transverse sinus and vena cerebralis media was present in *Eocaptorhinus* is confirmed by the existence of a prominent supratrigeminal process (promenentia vestibularis interna of Bruner, 1907), as in lizards and especially in turtles, and as developed to a lesser extent, in *Sphenodon*. The process floors the lateral intracranial passage through which the vena cerebralis media flowed from the transverse sinus to the trigeminal notch. The supra-trigeminal process is relatively longer in modern forms in which the vena cerebralis media is, at least in part, pre-trigeminal. The well-developed process in *Eocaptorhinus* thus indicates the former presence of at least a well developed pre-trigeminal and probably a large post-trigeminal division of the vena cerebralis media (Fig. 11). Both branches are believed to have emptied into the vena capitis lateralis as Grosser and Brezina (1895), Bruner (1907), and van Gelderen (1924) suggested.

<u>Vena tympanica anterior</u> (VTA)

In *Sphenodon* and lizards, a vena tympanica anterior connects the vena capitis lateralis (s.l.), just posterior to the vena cerebralis media (prima), to the vena mandibularis, anterior to the stapes and medial to the quadrate (Bruner, 1907; O'Donoghue, 1920) (Fig. 11). At about mid-length, the vena tympanica anterior gives rise to an anteroventrally projecting vena mandibularis interna. Additionally, in *Sphenodon* a small dorsal muscular ramus of the vena tympanica anterior drains the M. longissimus capitis (cervical musculature) through the post-temporal fenestrae and the tissues surrounding these fenestrae (O'Donoghue, 1920).

A vena tympanica anterior was not described or illustrated in the turtle *Emys orbicularis* by Bojanus (1819-21) nor was it mentioned by Bruner (1907) who noted that the mandibular vein and presumably its tributaries were not well known at that time nor are they well known even today. The presence or absence of a vena tympanica anterior in crocodilians has not been noted.

Since the roots of the sub-thecodont teeth of *Eocaptorhinus* were apparently drained by an internal mandibular vein similar to that of *Sphenodon* it is thought likely that the vein drained into a vena tympanica anterior just as it does in *Sphenodon* and lizards (Fig. 6). In addition, the primitively open middle ear cavity of *Eocaptorhinus* is similar to that of *Sphenodon* and lizards in allowing direct contact between the vena capitis lateralis and vena mandibularis. This is a markedly different pattern from that seen in modern turtles wherein the middle ear cavity is excluded from access to the adductor fossa by the posteromedial expansion of the pterygoid that forms the floor of the encapsulated middle ear region and, thus, leading to the loss of the vena tympanica anterior. It seems likely that the vena tympanica anterior has been lost in crocodilians because of similar remodelling of the braincase.

Vena cerebralis posterior (VCP)

The vena cerebralis posterior of modern reptiles drains deoxygenated blood posteriorly through the occiput from the intracranial, sinus longitudinalis cerebri (sinus occipitalis posterior of Dendy, 1909) to the vena capitis lateralis (Figs. 11 and 12). In turtles, the vena cerebralis posterior has two branches, a small one that leaves the braincase through the vagus (jugular) foramen accompanied by the vagus nerve (X), and a larger ramus that exits through the ventrolateral portion of the foramen magnum (Bojanus, 1819-21; Bruner, 1907). In addition, a large dorsal vena occipitotemporalis (sinus occipitalis of Bojanus, 1819-21) leaves the dorsal portion of the foramen magnum and invests the dorsal region of the temporal musculature within the emarginated temporal region, if present, from which region it drains posteroventrally into the vena jugularis communis (Bojanus, 1819-21). It appears that the development of the vena occipitotemporalis is a uniquely derived chelonian character, not a primitive pattern. The existence of two outlets for the sinus longitudinalis cerebri, one through the vagus foramen, the other through the foramen magnum, is believed to be the primitive condition.

In *Sphenodon* only the branch of the vena cerebralis posterior exiting through the vagus foramen is retained (Dendy, 1909; O'Donoghue, 1920) while in lizards (except amphisbaenids), only the ramus leaving the head through the foramen magnum remains.

The large size of the vagus foramen in *Eocaptorhinus* suggests that a substantial branch of the vena cerebralis posterior accompanied the vagus nerve (X) and probably the vagus accessory (XI) through the foramen (Figs. 4, 5, and 6). In addition, *Eocaptorhinus*, like many other primitive reptiles, had a well developed facet on the exoccipital that articulated with the proatlas, a vertebral element absent in all modern reptiles (Price, 1935; Romer and Price, 1940; Carroll, 1969a; Heaton, 1975, 1978). This facet along the lateral edge of the foramen magnum was separated from the occipital condyle by a prominent opening through which a well developed spinal branch of the vena cerebralis posterior is believed to have passed. The vagus and spinal branches probably united before joining the vena capitis lateralis anterior to its junction with the mandibular vein to form the vena jugularis communis. Additionally, a small occipital vein may have drained the occipital region into the base of the vena cerebralis posterior as in *Sphenodon* (O'Donoghue, 1920) but this cannot be confirmed.

Vena pterygoidei (VPT)

In all modern reptiles the pterygoid vein drains both the dorsal surface of the palate including interpterygoid vacuities (where present) and the lateral palatine sinus through a moderate to very large suborbital fenestra (Figs. 11 and 12). This is demonstrably a derived character that may have developed separately in both turtles and in diapsid reptiles, for the most primitive reptiles had either only an extremely small suborbital fenestra, as do the captorhinomorphs, procolophonoids, and paraiessaurs, or no fenestra at all as is characteristic of pelycosaurs. Of modern reptiles, only *Sphenodon* has a pterygoid vein that bears any similarity to that suspected to have been present in more primitive forms. In *Sphenodon* the pterygoid vein drains the dorsal surface of the palate and the interpterygoid vacuity beneath the inferior orbital membrane in the region where blood is supplied by the palatine artery. The pterygoid vein extends posteriorly to the medial corner of the suborbital foramen where a short ventrolateral connection with the lateral palatine sinus is made through the foramen. It continues posteromedially to join the vena capitis lateralis medial to the epipterygoid.

Since it is presumed that the dorsal surface of the palate of *Eocaptorhinus* must, somehow, have been drained of deoxygenated blood and, since a pterygoid vein, albeit in highly modified form, is common to all modern reptiles, a pterygoid vein similar to that of *Sphenodon* without the ventral connection with the lateral palatine sinus, has been reconstructed (Fig. 5).

Sinus orbitalis (SOR)

Both *Sphenodon* and lizards have well developed orbital sinuses that lie between the ball of the eye and its adnexa, and the periorbital membrane medially, suborbital membrane ventrally, and orbitotemporal membrane posteriorly. They do not usually invest the anterior portion of the orbit, this room being occupied by the orbital adnexa, including the nictitating membrane, Harder's Gland, superior and inferior oblique muscles, several nerves, a number of arteries, the conjunctiva and the lachrymal ducts (Bruner, 1907; O'Donoghue, 1920; Underwood, 1970). The orbital sinus is formed of a number of thinwalled sacs that have apparently developed by expansion of primitive ophthalmic veins as are present in modern fish and amphibians. The difference in terminology between what is considered to be a vein and what a sinus is purely subjective. In general, a sinus, such as the orbital sinus, is a loose anastomotic network of thinwalled venous channels that is often perforated to allow passage of muscles (e.g. the rectus, bursalis, and retractor bulbi musculature), nerves (e.g. optic, oculomotor, trochlear, and trigeminal nerves), and arteries (e.g. ophthalamic, orbital, and inferior orbital arteries). The orbital sinus drains ventroposteromedially into the anterior end of the vena capitis lateralis (sensu lato). It collects blood from the vena palpebrae inferioris (VPI), vena supratemporalis (VST), vena frontalis (VFR), vena praefrontalis (VPF), vena orbitonasalis (VON), and vena maxillaris (VMX) and additionally, in lizards, develops a secondary connection with the vena cerebralis media secunda (Bruner, 1907; O'Donoghue, 1920) Figs. 11 and 12).

In turtles the orbital sinus appears to be simpler than in *Sphenodon* and lizards. Bojanus (1819-21), the only person to illustrate the orbital drainage system in turtles, referred to numerous "venae ophthalmicae" while Underwood (1970) regards these veins as parts of an orbital sinus similar to that of lepidosaurs. With the great reduction in the length of the snout and loss of the septomaxilla in all and the nasal in most turtles, extreme differences in preorbital drainage are seen. The intracranial sinus falciformis serves as the major drainage channel from the snout (Bojanus, 1819-21). This is not, however, believed to be a primitive dondition. The orbital drainage of crocodilians has not been described (Underwood, 1970).

There is little direct evidence of an orbital sinus in *Eocaptorhinus*. Well developed foramina, channels, and canals that apparently carried typically lepidosaurian inferior palpebral, frontal, and orbitonasal veins provide solid associated evidence for the assumed presence of a lepidosaur-like orbital sinus draining posteriorly through the vena capitis lateralis (s.l.).

<u>Vena palpebralis inferior</u> (VPI)

Bruner (1907) described an inferior palpebral vein in lizards that drained the region of the lower eyelid and the lachrymal duct between, and just medial to, the lachrymal puncti and lateral to the anterior orbital artery. An inferior palpebral vein has not been described in other reptiles, probably because of its small size.

In *Eocaptorhinus*, where the lachrymal is heavily ossified and encloses the lachrymal duct and associated blood vessels, there is a small foramen and canal that enters the lachrymal about midway between and slightly medial to the lachrymal puncti and just lateral to the anterior orbital canal which is believed to have carried the anterior orbital artery. It is believed that this small canal carried the anterior extremity of an inferior palpebral vein.

Vena frontalis (VFR)

A well developed vena frontalis is present in both *Sphenodon* and lizards (Bruner, 1907; O'Donoghue, 1920). In *Sphenodon* it is formed from the junction of an anterior and a posterior branch entering the dorsal rim of the orbital sinus while in lizards, only the anterior branch is developed. This vein perforates the frontal and drains it and its overlying tissues. In lizards fine lateral supraorbital branches drain the supraorbital tissues.

Small foramina in the orbital rim portion of the frontal and prefrontal of *Eocaptorhinus* lateral to the solum supraseptale are believed to mark the points where the frontal artery or its branches entered the bone.

Vena orbitonasalis (VON)

Amongst modern reptiles, only *Sphenodon* retains a primitive orbitonasal vein that joins the superior premaxillary sinus and the nasal sinus to the orbital sinus. In lizards this vein is much reduced, draining the posterodorsal portion of the nasal capsule, and is not connected to the superior premaxillary vein. In turtles the orbitonasal vein has been lost, at least in part because of the assumption of the snout drainage functions by the intracranial falciform sinus and its anterior nasal venules. The specific nature of the drainage of the snout of crocodilians is unknown but is expected to be highly modified as a consequence of the remodelling of the snout and the development of the secondary palate.

In *Eocaptorhinus* the orbitonasal canal is a long osseous tube whose ventral surface forms the prominent orbitonasal ridge on the ventral surface of the nasal from the nasal-premaxilla suture, where it runs confluently with the dorsal extension of the rostral sinus within the premaxilla, posteriorly to open ventrally through the orbitonasal foramen just anterior to the nasal-frontal suture (Heaton, 1975, 1978) (Fig. 11). It is believed that this canal carried a well developed orbitonasal vein which, when it left the orbitonasal foramen, continued posteriorly in a shallow but sharply delineated groove in the ventral surface of the frontal to enter the anterodorsomedial corner of the orbital sinus. A short prefrontal vein is believed to have entered the orbitonasal vein just before it entered the orbital sinus. This cannot be confirmed for it is possible that the prefrontal vein entered the orbital sinus separately. The apparent close contact between the orbitonasal vein and the ventral surface of the frontal, as is suggested by the well marked groove, indicates that the orbitonasal vein passed dorsal to the nasal artery. Several small foramina in the ventromedial surface of the orbitonasal ridge may have served to transfer some blood from the nasal sinus to the orbitonasal vein although the quantity of blood so transported would have been small.

It is suspected that the presence of a well developed orbitonasal vein was characteristic of many or most captorhinomorphs including the ancestors of the modern diapsid lineages. The development of an osseous orbitonasal canal in captorhinids may be a specialized character of that group or it may represent a more primitive pattern associated with heavy bone development that has been lost in smaller, lighter forms with greatly reduced bone thickness. The available data are not sufficient to allow a decision to be made either way.

Vena praefrontalis (VPF)

The prefrontal vein of *Sphenodon* (part of the vena nasalis dorsalis of O'Donoghue, 1920) appears to be homologous with that of lizards (Bruner, 1907) even though that of *Sphenodon* drains into the orbital sinus just posteromedial to the inlet of the orbitonasal vein while that of lizards enters the orbitonasal vein just posterolateral to where it empties into the orbital sinus. Since the vein-sinus junction is not sharp, exact identification of the point of entry of the prefrontal vein is difficult. It is fully possible that further investigation will reveal substantial diversity in the development of this feature in modern reptiles. A prefrontal vein has not been described in either turtles or crocodilians.

A prefrontal vein appears to have collected blood from the anterior surface of the orbital rim section of the prefrontal of *Eocaptorhinus*, from which small branches seem to have emerged through several tiny foramina. As well, the ventral surface, and through it the skin, over the prefrontal and frontal bones appear to have been drained through this vein. A small vena nasalis dorsalis may have drained the posterodorsal region of the nasal capsule into the prefrontal vein as in *Sphenodon* or into the orbitonasal vein as in lizards. There is, however, no definite evidence for the presence of such a vein.

Vena supratemporalis (VST)

A supratemporal vein of similar form is present in both *Sphenodon* and lizards (Bruner, 1907; O'Donoghue, 1920). It conducts deoxygenated blood from the adductor musculature between the M. adductor mandibulae externus superficialis laterally and the M. pseudotemporalis superficialis medially, anteriorly into the posterodorsolateral corner of the orbital sinus. Posteriorly the vena supratemporalis is divided, with a short lateral branch extending between the M. adductor mandibulae pars superficialis laterally and the pars media medially and a short medial branch separating the M. adductor mandibulae externus medius posterolaterally and the M. pseudotemporalis superficialis anteromedially. This is the same type of pattern that is believed to have existed in *Eocaptorhinus* where the positions of the muscles are known with some certainty.

The drainage of the temporal region in turtles is considerably different, being derived from a loop of the cervical vein that has migrated anteriorly over the dorsal surface of the temporal musculature in the area of the posterodorsal emargination of the skull (where present), and being connected medially with the sinus longitudinalis posterior through the upper part of the foramen magnum (Bojanus, 1819-21).

Vena maxillaris (VMX)

In most modern reptiles, with the exception of snakes, the maxillary vein is a fine vessel that drains the alveolar portion of the maxillary tooth row posteriorly through the supramaxillary and superior alveolar canals (Figs. 11 and 12) to the infraorbital foramen. In *Sphenodon* and lizards it leaves the maxilla through this foramen and extends along the dorsomedial edge of the maxilla, dorsal to the palatine and suborbital foramen, and ventral to the orbital sinus. The posterior portion of the superior labial vein turns dorsomedially around the posterior end of the maxilla and the ectopterygoid, then pierces the orbitotemporal membrane to join the maxillary vein and extend dorsally to empty into the posteroventrolateral corner of the orbital sinus (Bruner, 1907; O'Donoghue, 1920).

The structure of the vena maxillaris of turtles is generally similar to that of *Sphenodon* and lizards, however, it exits onto the dorsal surface of the palate through a displaces supramaxillary foramen that is exposed within the orbit by the reduction and eventual loss of the lachrymal which forms the primitive dorsal rim of the infraorbital foramen. Associated with the loss of the primitive reptilian marginal dentition in modern turtles and the development of a keratinous beak is the absence of both a superior labial vein and, thus, any connections between the subpalatal drainage and the orbital sinus. It appears that the maxillary artery, upon reaching the posterior wall of the orbit turns medially across the dorsal surface of the palate where it joins the pterygoid vein and together enter the vena capitis lateralis (s.l.) independent of the orbital sinus (Bojanus, 1819-21).

The maxillary vein of *Eocaptorhinus* appears to have had characteristics of both lepidosaurs (except snakes) and turtles. It is believed to have drained posteriorly through the superior alveolar and supramaxillary canals from which it exited through the infraorbital fenestra onto the dorsal surface of the palate, essentially as in *Sphenodon* and lizards or, with the exception of the loss of the lachrymal, in turtles. The maxillary vein is believed to have emptied into the orbital sinus as in lepidosaurs (Figs. 11 and 12) rather than into the pterygoid vein as in turtles. This assessment has been made because of the generally greater apparent similarity of the cranial circulatory system of *Eocaptorhinus* to lepidosaurs than to turtles. There is, however, no hard evidence to confirm this reconstruction. The heavy sculpturing of the lateral surface of the maxilla is associated with the internal drainage of the skin into the maxillary vein and with the probable absence of a superior labial vein. Heavy sculpturing and the apparent absence of a superior labial vein is characteristic of many groups of primitive reptiles.

Sinus rostralis (SRO)

The rostral sinus of lizards is a short, horizontal expanded vein that lies across the anterior face of the premaxilla and communicates posteriorly with the superior premaxillary sinus by means of a very short medial nasal vein that passes through the posterior premaxillary foramen (Bruner, 1907; Oelrich, 1956; Heaton, 1975, 1978). Bruner has shown that the rostral sinus does not drain laterally into the superior labial vein.

O'Donoghue (1920) described as the sinus rostralis of *Sphenodon*, a small sinus that lies behind and above the premaxilla that appears actually to be the superior premaxillary sinus, hence its drainage into the maxillary and superior labial vein. It appears that there is no rostral sinus in *Sphenodon*, the skin covering the anterior surface of the premaxilla being drained through fine venules into the superior labial vein.

The venous drainage of the snout is not well known in either turtles or crocodiles.

Eocaptorhinus appears to have had a larger rostral sinus enclosed within the body of the premaxilla. It was connected posteriorly to the superior premaxillary sinus through the large posterior premaxillary foramen just as in lizards, and like them, did not drain laterally into the superior labial vein or the maxillary vein. The skin covering the premaxilla drained internally through numerous fine pores in the well developed sculpture pits into the sinus rostralis. Additionally, the sinus rostralis communicated dorsally through the orbitonasal canal of the nasal and the nasal ramus of the premaxilla and with the orbitonasal vein. If the development of the orbitonasal vein-rostral sinus is typical of all captorhinomorphs, a point that cannot as yet be confirmed, it appears that during the apparent captorhinomorph-diapsid transition extensive reduction of the external layer of lamellar bone of the premaxilla occurred until the rostral sinus was exposed externally as in lizards or lost as in *Sphenodon*.

Sinus praemaxillaris superior (SPS)

Sphenodon and lizards both possess a small sinus that lies transversely across the dorsal surface of the vomerine process of the premaxillae. Bruner (1907) illustrated it just posterior to the rostral sinus, to which it is connected by a pair of short veins that pass through the posterior premaxillary foramina. He did not name this sinus, however, possibly because he regarded it as a continuation of the maxillary vein although this point is not clear. O'Donoghue (1920) recognized the same sinus in *Sphenodon* but mistakenly referred to it as the rostral vein (sinus) which it is not since it lies within the nasal region, not within or anterior to the premaxilla. In fact, as noted above, *Sphenodon* does not appear to have a rostral sinus. In lizards the superior premaxillary sinus is situated anterodorsal to the prepalatal foramina through which it discharges blood into the lateral palatine and transverse palatine sinuses. Laterally, the superior premaxillary sinus empties into both the superior labial vein and the maxillary vein. The drainage of the premaxillary region in *Sphenodon* appears to be similar except for the absence of any prepalatal foramina. O'Donoghue (1920) has indicated that there is a connection between the superior premaxillary sinus and the nasal sinus. It is not known how the connection between the transverse palatine sinus and the superior premaxillary vein was effected, as O'Donoghue (1920) indicates it was, unless passage was made through the most anterior extremity of the internal naris. In any case, the superior premaxillary vein empties into the superior labial and maxillary veins in *Sphenodon*, also.

Eocaptorhinus appears to have had a superior premaxillary sinus similar in position to that of lizards but different in function. Where in *Sphenodon* and lizards this sinus drains posteriorly into the lateral palatal sinuses and posterolaterally into maxillary and superior labial veins, in *Eocaptorhinus* it appears that the direction of flow was reversed with the lateral and medial palatine sinuses draining anteriorly into the superior premaxillary sinus thence into the rostral sinus and the orbitonasal vein. There appears to have been no superior labial vein in *Eocaptorhinus* and no connection to the maxillary vein.

Sinus nasalis (SNA)

The nasal sinus is a loose aggregation of venous channels and connective tissue that forms the spongy tissues that surround and line the cartilaginous vestibule of the nasal capsule in both *Sphenodon* and lizards (Bruner, 1907; O'Donoghue, 1920). It drains laterally into the maxillary vein. In *Sphenodon* the principle drainage of the nasal sinus takes place through the prominent orbitonasal vein. In addition, the nasal sinus of *Sphenodon* is connected directly to the superior premaxillary sinus (O'Donoghue, 1920). Lizards have neither a connection with an orbitonasal vein nor with the superior premaxillary foramen.

The vestibule of the nasal capsule of *Eocaptorhinus* can be reconstructed easily within the conical tube of the septomaxilla. The nasal sinus lined the vestibule as well as that portion of the snout anterior to the vestibule and its enclosing septomaxilla. The septomaxilla meets the nasal, lachrymal and maxilla along its posterolateral edge, thus preventing access of the nasal sinus to the post-vestibular region of the maxilla. This, combined with the absence of an anterior opening of the superior alveolar canal, confirms the absence of any connection between the nasal sinus and the maxillary vein. Small foramina are present in the ventral surface of the orbitonasal ridge thus indicating a minor amount of drainage of the nasal sinus into the orbitonasal vein. Although the nasal sinus was relatively smaller than that of modern lepidosaurs because of the more anterior position of the septomaxilla and enclosed vestibule of the nasal capsule, it is apparent that the dorsal access to the orbitonasal vein was not sufficient to accommodate the total drainage of the nasal sinus. It thus appears that the principal flow of deoxygenated blood from the nasal sinus took place into the superior premaxillary sinus and thence to the orbitonasal vein by way of the large posterior premaxillary foramina.

Sinus palatinus transversus (SPT)

The sinus palatinus transversus anterior of both *Sphenodon* and lizards is similar, lying ventral to the vomerine processes of the premaxillae and divided into anterior and posterior parts by the incisive process. It receives blood from the medial palatine sinus and the superior premaxillary sinus. Deoxygenated blood flows from it into the lateral palatine sinuses (Bruner, 1907; O'Donoghue, 1920). In *Sphenodon* there is a small connection between the transverse palatine sinus and the nasal sinus that apparently is absent in lizards. The direction of flow through this short vein is not known although it may be variable. The pattern of venous drainage in the snout region of turtles and crocodilians has not been described adequately.

Eocaptorhinus appears to have had a transverse palatine sinus similar in general form to that of *Sphenodon* and lizards. It is not known whether this sinus was divided into anterior and posterior parts, as it is by the incisive process in lizards. Since it is apparent that the nasal sinus of *Eocaptorhinus* did not drain principally into the orbitonasal vein as it does in *Sphenodon*, a connection with either the superior premaxillary or transverse palatine sinus, or both, is regarded as a functional necessity.

Sinus palatinus medius (SPM)

The medial palatine sinus of both *Sphenodon* and lizards is generally similar in form. It is a long median vein running from the anterior rim of the interpterygoid vacuities anteriorly, medial to the internal nares to join the sinus transversus palatinus. The palatal drainage systems of turtles and crocodilians have not been described or illustrated.

In *Eocaptorhinus* the left and right halves of the palate meet in a deep "V"-shaped trough, anterior to the interpterygoid vacuities, that it believed to have held a large medial palatine sinus (Fig. 14).

Sinus palatinus lateralis (SPL)

Modern lizards and *Sphenodon* have well developed lateral palatine sinuses that drain posterior by way of the pterygoid vein into the vena capitis lateralis by way of the large suborbital fenestrae (Bruner, 1907; O'Donoghue, 1920). The lateral palatine sinus is a loose network of thin-walled veins that may be roughly divided into anterior and posterior portions. The anterior segment covers the ventral surface of the vomer and anterior end of the palatine within the incisive pad as well as investing much of the choanal tissue lining the internal naris. It is divided laterally by the choanal cleft which it surrounds. O'Donoghue (1920) has illustrated a venous connection between the intrachoanal lateral palatine sinus and the extrachoanalnasal sinus in *Sphenodon* but this has not been confirmed. Bruner (1907) did not describe such a connection in lizards. The lateral palatine sinus is constricted just posterior to the internal naris before again expanding to cover the ventral surface of the palatine and pterygoid. The palatal tooth rows, when well developed, perforate the lateral palatine sinus. The lateral palatine sinuses of *Sphenodon* and lizards are constricted posterolaterally where they join the pterygoid vein through the large suborbital foramen and, thus, drain into the vena capitis lateralis.

Bruner (1907) has briefly described both medial and lateral palatine sinuses in the turtle *Emys orbicularis*. He notes many unusual relationships with other veins. His lack of illustrations of the venous system of *Emys*

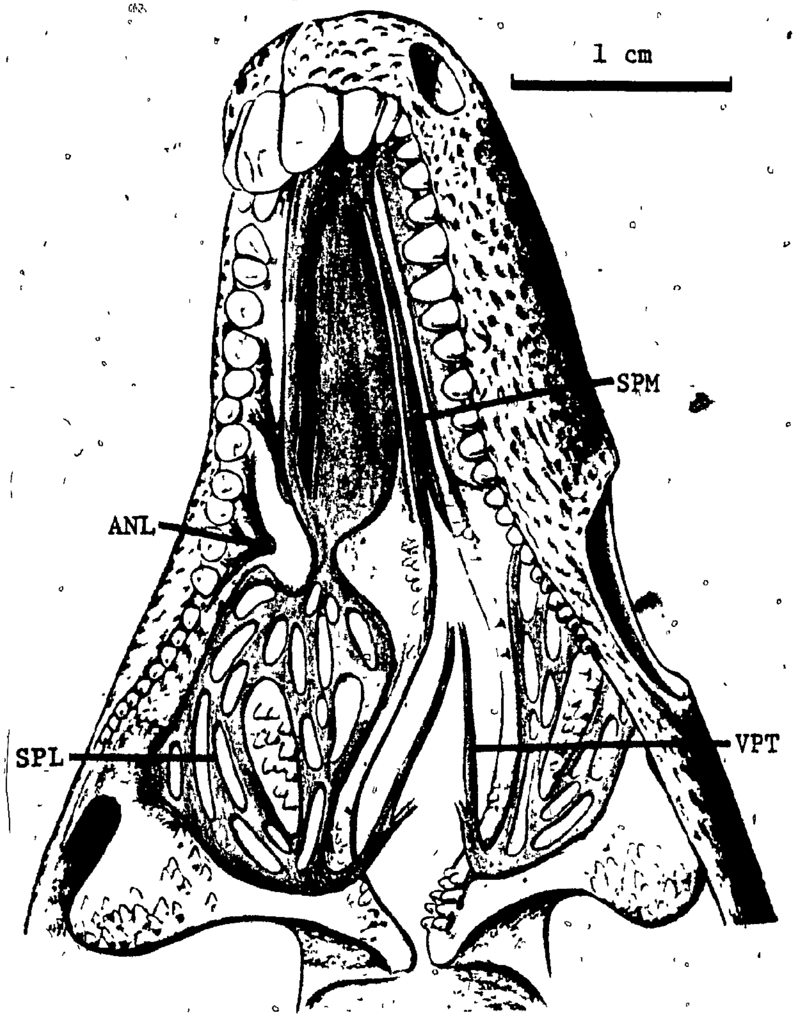


Figure 14. *Eocaptorhinus laticeps*. Palate in ventral aspect showing lateral palatal sinuses. Reconstruction.

and its relationship to the bones of the skull makes interpretation of this description difficult. It appears that Bruner is indicating a connection between the lateral palatine sinus and the orbital sinus through the posterior palatine foramen (suborbital fenestra). Bojanus (1819-21) illustrated a branched palatine vein, that appears to correspond to Bruner's sinus palatinus lateralis, that drained through the posterior palatine foramen directly into the vena capitis lateralis. Obviously considerable study of the cranial venous systems of modern turtles needs to be done, although a basic similarity to other modern reptiles is apparent. Nothing has been reported of the crocodilian pattern of palatal drainage.

Two clearly demarked, smooth, and slightly depressed regions of the ventral surface of the palate of *Eocaptorhinus* appear to reflect a division of a well developed lateral palatine sinus just as in *Sphenodon* and lizards. Except for the greater development of the palatal tooth fields in *Eocaptorhinus* which must surely have extended through the sinuses as separate "islands" of teeth, differences are small. The drainage of blood from the lateral palatine sinuses must, however, have been vastly different for, in the absence of a large suborbital fenestra, as is present in all modern reptiles, there could have been no passage of blood from the palate posterodorsally through the pterygoid vein into vena capitis lateralis. Some, and perhaps all, of the blood from the palate appears to have drained anteriorly into the transverse palatine sinus, thence dorsally through the prepalatal foramina into the superior premaxillary sinus and then through the posterior premaxillary foramina to the rostral sinuses (Fig. 14). It is possible that, in view of the relatively small size of the prepalatal foramina, that some blood drained from the transverse palatine sinus to superior premaxillary sinus through the anterior end of the internal naris as O'Donoghue (1920) described in *Sphenodon* although this is regarded with suspicion. The main route of palatal drainage appears to have been anteriorly to the rostral sinus thence posterodorsally through the large orbitonasal vein to the orbital sinus. It is possible that the lateral palatine sinus drained posterolaterally into the external mandibular vein but such a course cannot be confirmed.

Vena mandibularis (VMD)

The mandibular vein of modern reptiles drains the posterior region of the mandible and the tympanic cavity into the vena capitis lateralis at about the same position as the entrance of the vena cerebralis posterior. Distally it passes lateral to the quadrate, and through the quadrate foramen in *Sphenodon*. In *Sphenodon* and lizards it then receives the anastomotic, anterior tympanic vein before separating to form an external mandibular vein (VME) and a connection to the internal mandibular vein (VMI). The extensive remodelling of the skull in turtles has led to the loss of the anterior tympanic vein.

The large quadrate foramen in *Eocaptorhinus* appears to have carried a well developed mandibular vein as in *Sphenodon*.

Vena mandibularis externa (VME)

In *Sphenodon* and lizards, the external mandibular vein runs anteroventrally along the lateral surface of the mandible just ventral to the origin of the M. adductor mandibulae externus superficialis, including the M. levator anguli oris, and then continues forward along the lateral edge of the crista dentalis of the dentary where it drains the skin and mandibular labial glands (Bruner, 1907; O'Donoghue, 1920). Anterior to the mandibular articulation, the external mandibular artery receives the anastomotic, anterior tympanic vein. Just forward of this point, a medial connection is made with the internal mandibular artery (Bruner, 1907). In lizards, this short vein passes dorsal to the mandibule and posterior to the M. adductor mandibulae externus superficialis while in *Sphenodon*, the surangular has expanded anterodorsally and the dentary posterodorsally to form an arch that encloses the surangular foramen through which passes the small connecting vein.

In turtles, the external mandibular vein arises from a bifurcation of the mandibular artery that also produces a large posterior tympanic vein similar to that of *Sphenodon* and lizards. The main extension of the external mandibular vein runs anteriorly lateral to the quadrate and ventral to the insertion of the M. adductor mandibulae externus superficialis. It drains the skin covering the lower surface of the mandible. Unlike lepidosaurs, turtles have a dorsal branch of the external mandibular artery that extends up the anterior edge of the M. adductor mandibulae externus superficialis to the level of the dentofacial foramen. The function of this foramen has not been recorded in print, principally because of the difficulty of dissecting through the heavy bone of the mandible, but it appears to have accommodated a connection between the internal mandibular vein and the external mandibular vein. In addition, in the many advanced turtles that have lost the proximal region of the mandibular artery and in which the adductor fossa is greatly reduced, a ventral extension of the inferior orbital artery may pass through this foramen to join the internal mandibular artery.

Eocaptorhinus is presumed to have had an external mandibular vein that extended from the quadrate foramen along the lateral surface of the mandible just ventral to the insertion of the M. adductor mandibulae externus superficialis, including the M. levator anguli oris and M. retractor anguli oris. It may have continued anteriorly along the dorsal edge of the dentary lateral to the crista dentalis to drain the labial glands but this seems unlikely. The heavily developed pit-and-ridge sculpturing of the lateral surface of the mandible indicates that most of the skin overlying this region drained internally rather than through the external mandibular vein. It is possible that a branch of the external mandibular vein turned dorsally along the anterior edge of the M. adductor mandibulae externus superficialis possibly even joining the posterolateral corner of the lateral palatine sinus in order to supplement the palatal drainage although this cannot be confirmed.

Vena mandibularis internus (VMI).

In lizards, the internal mandibular vein has two major branches, one dorsal, the other ventral. The dorsal branch originates from the mid-point of the anterior tympanic vein and extends anteriorly through the Meckelian canal dorsal to the Meckelian cartilage. Anteriorly it is intraosseous, lying within the inferior alveolar canal with the inferior alveolar artery and nerve (Bruner, 1907). *Sphenodon* has an internal mandibular vein similar to the dorsal branch of lizards. O'Donoghue (1920) did not describe a ventral branch in *Sphenodon* such as exists in lizards. In lizards, the ventral branch extends from the sinus articularis, a secondary ventral anastomosis between the external mandibular vein and the dorsal branch of the internal mandibular vein, forward to drain the symphysial region.

The structure of the internal mandibular vein is not known in any detail in either turtles or crocodiles.

Since the structure of the mandible in *Eocaptorhinus* is, except for its more robust construction, similar to that of lizards, a generally lizard-like internal mandibular vein has been reconstructed with a dorsal branch draining the dentary through the inferior alveolar canal and a ventral branch draining the region of the jaw symphasis as well as the insertion of the M. intramandibularis.

Discussion

The cranial arterial systems of modern reptiles are, with the exception of those of crocodilians and some turtles, similar in form. In *Eocaptorhinus* few differences from *Sphenodon* or lizards can be traced in the postorbital arterial system. Nevertheless, a few primitive characteristics are to be noted. In *Eocaptorhinus* the palatine branch of the internal carotid accompanied the vidian (palatine) ramus of the facial nerve through a deep vidian sulcus in the ventral surface of the basipterygoid process at the junction of the basisphenoid and parasphenoid. An open vidian sulcus is a common feature seen in primitive temnospondyl (Shishkin, 1968) and anthracosaurian amphibians (Panchen, 1964, 1970) as well as in captorhinomorphs and pelycosaurs (Romer and Price, 1940). A distinct enclosed vidian canal has developed independently in stereospondyl amphibians (Shishkin, 1968) and in modern turtles, crocodilians, and lepidosaurs. In lepidosaurs, a relatively short vidian canal has formed by lateral expansion of the parasphenoid ventral to the vidian nerve and palatine artery to join and fuse with the basisphenoid of the basipterygoid process. The vidian canal is much longer in modern turtles and is often connected to a separate internal carotid canal (Gaffney, 1972). The evolutionary events leading to the diverse forms of vidian canals in modern turtles are not well known. The highly modified braincase of crocodilians has not allowed the history of the development of the internal carotid (vidian) canal to be traced in any detail. The structure of the vidian sulcus in *Eocaptorhinus* and other captorhinomorphs is sufficiently primitive that any of the modern vidian or internal carotid canals could have developed from it.

The temporal artery of the most primitive reptiles was a continuation of the stapedial artery after it passed the dorsal edge of the quadrate and entered the adductor chamber between the origins of the partes media A and B of the M. adductor mandibulae externus just as it does in modern *Sphenodon* and lizards. In forms such as the captorhinomorphs where the partes media A and B were well developed, a short dorsal temporoparietal branch of the temporal artery evolved to supply blood to the origins of these muscle segments and to the skin covering the parietal through a temporoparietal foramen in the ventral surface of that bone. In reptiles in which either the pars media B (turtles) or the partes media and profunda (synapsids) of the M. adductor mandibulae externus were absent, no temporoparietal artery or foramen developed. It is believed that the temporoparietal foramen of captorhinomorphs served, in small forms with very lightly built skulls, as the locus about which the upper temporal fenestra of diapsids developed. Iguanid lizards possess a small dorsolateral branch of the temporal artery in the exact position of the temporoparietal foramen and presumed artery in *Eocaptorhinus* that may be homologous with the primitive temporoparietal artery.

The infraorbital artery is a major anterior branch of the temporal artery in most reptiles. It exhibits diverse patterns of division and passage into the snout region. *Eocaptorhinus* appears to have had an infraorbital artery that was almost identical to that seen in many modern turtles. With the reduction and subsequent loss of the septomaxilla and the nasal ramus of the premaxilla, the subnarial and postnarial branches of the maxillary artery of turtles have been lost. The chelonian prepalatal foramina transmit terminal branches of the anterior nasal artery (Bojanus, 1819-21; Albrecht, 1967; Gaffney, 1972) and are positioned more posterior than they were in *Eocaptorhinus* indicating that they may not be homologous structures. The pattern in crocodilians appears to be similar to that of turtles. The postnarial artery disappeared with the loss of the septomaxilla while the subnarial artery remains rather large. The extensive modification of the maxilla inherent in the development of the crocodilian secondary palate makes other comparisons difficult. The pattern of branching of the infraorbital artery in lizards is confused by the generally lighter bone structure that has led to the loss of some of the distinctive canals through which specific arteries pass and which aid in the identification of these arteries. While descriptions of lizard cranial anatomy are relatively common, few have been detailed enough to reveal the exact structure of the maxillae and the associated arteries. In animals with thick dermal bone (captorhinids, turtles, crocodiles), there is a well formed separation between the courses of the maxillary artery and the supramaxillary and superior alveolar arteries laterally. The maxillary artery is not enclosed in bony canals in these forms. In many lizards, however, the great reduction in bone thickness correlated with the development of a pleurodont dentition has allowed the maxillary, supramaxillary, and superior alveolar arteries to come in contact with each other to form an arterial plexus supplying blood to the skin of the snout, the "lips" and the dental lamina. In *Sphenodon* and lizards with acrodont dentitions (Agamidae and Chamaeleontidae) the maxillary and supramaxillary arteries maintain their primitive positions.

While it appears from the literature (Oelrich, 1956) that the supramaxillary artery degenerated in pleurodont lizards, the superior alveolar artery may not have, at least if the superior alveolar arteries of both turtles and lizards are homologous as is often believed. There is reason to think that such a homology may not exist. In turtles, the superior alveolar artery does not enter the external naris or form a subnarial artery but instead ends abruptly. The superior alveolar artery of lizards, on the other hand, becomes the subnarial artery and crosses the ventral surface of the external naris just as the maxillary artery of *Eocaptorhinus* may have. It appears that pleurodont lizards, rather than having developed a new anterior superior alveolar foramen and new postnarial and subnarial arteries to replace analogous branches of the maxillary artery in captorhinomorphs, had a superior alveolar artery that degenerated in the same manner as did the supramaxillary artery with the loss of the superior alveolar canal. The canal referred to as the superior alveolar canal in lizards is a neomorph, preferably called the maxillary canal, and has evolved by a vertical extension of the captorhinomorph septomaxillary tubercle dorsally to contact the dorsal process of the maxilla and thus enclose the maxillary artery.

The pattern of branches of the maxillary artery in *Sphenodon* is determined by the presence of an acrodont dentition. As in agamid lizards, a prominent supramaxillary artery runs forward within the infraorbital canal and what was primitively the superior alveolar canal. There is no maxillary artery and thus no superior alveolar artery, its function having been taken over by the anterior extension of the supramaxillary artery, and no maxillary canal. It is obvious that there is a very close correlation between the patterns of inferior orbital artery branching and the type of tooth emplacement in any reptiles group but such a discussion is well beyond the scope of this paper.

In all modern reptiles, the inferior palatal artery passes through the suborbital fenestra to nourish the posterior region of the oral mucosa. In *Eocaptorhinus*, if this artery existed at all, it was extremely small. Pelycosaurs, the earliest known synapsid reptiles, never developed or had lost the primitive small suborbital fenestra and, as a result, did not have an inferior palatal artery.

Any analysis of the pattern of cranial veins and their importance in primitive reptiles is hampered by the paucity of incontrovertible evidence pertaining to them and by the consequent need to make subjective decisions based on a knowledge of the anatomy of modern reptiles. With this in mind, certain conclusions can be based on the described positions of the cranial veins of *Eocaptorhinus*.

The general configuration of the braincase, palate, and snout of *Eocaptorhinus* is similar to that of lizards, *Sphenodon*, and, to a lesser degree, turtles, although individual differences do occur. The principal course of venous drainage from the head of *Eocaptorhinus* is thought to have been a large vena capitis lateralis that collected blood from within the braincase and chondrocranium and from the orbit just as in modern lepidosaurs and turtles. Few differences are noted in this area that are of significance to this discussion save that the vena cerebralis posterior of *Eocaptorhinus* appears to have exited through the foramen magnum.

It is difficult to determine just what form the orbital sinus took. In lizards and *Sphenodon* large thin-walled sinuses are the rule. In turtles, particularly *Emys*, the only form to have been investigated even superficially, Bruner (1907) described a lizard-like orbital sinus with which Underwood (1970) agreed, while Bojanus (1819-21) showed separate veins, the ophthalmic veins, running through the orbit. Presumably the sinuses developed from the more primitive system of ophthalmic veins similar to those seen in modern amphibians and mammals. Underwood (1970) has noted that there is no mention in the literature of the venous drainage of the orbit in crocodilians. While it is not possible to say positively whether a fully developed lizard-like orbital sinus existed in *Eocaptorhinus*, it does seem probable, and is so described, since it is possible to identify many peripheral veins of distinctly lepidosaurian form that drained into it.

The orbitonasal vein of *Eocaptorhinus* connected the rostral sinus to the orbital sinus just as in frogs (Gaupp, 1896-1901). The captorhinomorphs appear to be relatively primitive amongst non-synapsid reptiles in having the orbitonasal vein completely enclosed in a bony canal. In *Sphenodon*, the vein, called a sinus by O'Donoghue (1920), is much smaller and is not enclosed. The orbitonasal vein has been lost in lizards. Concommitant with the reduced importance of the orbitonasal vein in the captorhinomorph-lizard line is the development and elaboration of the pterygoid vein. There has been a complete reorientation of the venous drainage of the palate from an anterior drainage through the rostral and nasal sinuses and then posterior through the orbitonasal vein into the orbital sinuses to a posterior drainage of the palate and ventral snout through the lateral palatal sinuses and the lateral pterygoid vein. In captorhinomorphs the suborbital fenestra apparently carried only the inferior palatine artery and nerve. In all diapsids including the oldest known form *Petrolacosaurus* (Reisz, 1975, 1977), the suborbital fenestra is much larger so that the lateral palatine sinus was in close proximity to the dorsomedial pterygoid vein that drained the suborbital membranes. A connection between the lateral palatine sinus and the pterygoid vein was effected and soon became the principal means of palatal drainage. Once this pattern had developed, communication between the lateral palatal sinus and the maxillary vein, as occurs in lizards (Bruner, 1907) could be effected.

Well developed medial and lateral palatal sinuses appear to have been present in ophiacodont and sphenacodont and in some (caseid) edaphosaurian pelycosaurs where they covered the palate between the palatal tooth fields. All pelycosaurs lack suborbital fenestrae and thus did not drain these sinuses posterodorsally into the vena capitis lateralis through a pterygoid vein as do modern *Sphenodon* (O'Donoghue, 1920), lizards, and turtles (Bojanus, 1819-21; Bruner, 1907). Pelycosaurs also lack prepalatal and posterior premaxillary foramina as well as the orbitonasal canal as are present in captorhinomorphs and procolophonids (Ivakhnenko, 1973) thus indicating that a primitive saurian drainage of the palate through the snout did not occur. It is remotely possible that the lateral palatal sinus may have drained dorsally into the nasal sinus through the internal naris. The nasal sinus lies anterior and external to the vestibulum of the nasal casule in reptiles. In sphenacodontid pelycsoaurs, the position of the vestibulum is indicated by the presence of a large septomaxilla that would have precluded a connection between the intraconchal lateral palatal sinus and the extraconchal nasal sinus, if the latter even existed. The alternative to draining the lateral palatal sinus internally is to drain it externally into the external mandibular vein. The drainage of the ventral surface of the palate posteriorly into the external mandibular vein is thought to have been a typical synapsid character and is, in fact, probably homologous with the vena facialis profunda and proximal portion of the vena facialis externa of mammals. The lack, in sphenacodontid pelycosaurs of deep pit and ridge sculpturing with perforating pores that is common amongst primitive non-synapsid reptiles (Carroll and Baird, 1972; Clark and Carroll, 1973; Heaton, 1975, 1978) suggests the posibility that the skin covering the jugal, lachrymal, and prefrontal and the posterior portion of the maxilla of sphenacodontid pelycosaurs such as *Dimetrodon* (Romer and Price, 1940) was drained by a superficial vein not unlike the superior labial vein of *Sphenodon* and lizards (Bruner, 1907; O'Donoghue, 1920) but not connected internally with the orbital or palatal sinuses. This external vein that may have drained ventrally into the external mandibular vein, is thought to have been the precursor of the mammalian vena nasalis externa. The well developed prefrontal ridge of sphenacodontids indicates that the vena nasalis externa had not as yet developed a posterodorsal vena nasofrontalis. The premaxilla and pre-caniniform region of the maxilla apparently drained internally through pronounced pits and pores into the superior alveolar canal and into the superior alveolar and supramaxillary divisions of the maxillary vein in the primitive manner.

It is difficult to determine whether a well developed orbital sinus existed in pelycosaurs but it is expected that it did not. In contrast to the low, oblong orbits of *Eocaptorhinus* and many diapsids that accommodated large sinuses anterior and, especially posterior to the bulb of the eye, pelycosaurs have noticeably higher, rounder orbits with significantly less room for the sinuses. The lack of orbital sinuses, surely a primitive characteristic, is strongly correlated with the absence of the palatal drainage into the orbit as is characteristic of non-synapsid reptiles.

Conclusions

The cranial arterial system of *Eocaptorhinus* is of a primitive pattern from which the arterial systems of all modern reptiles could have developed. The vidian or internal carotid canal of modern reptiles had not yet developed, in its place was a deep vidian sulcus between the basisphenoid and the parasphenoid. A prominent temporoparietal branch of the temporal artery pierced the parietal posterior to supply the skin and the origins of the M. adductor mandibulae externus medius in captorhinomorphs. The foramen through which it passed may have formed the locus about which the dorsal temporal fenestra of araeoscelids and diapsids developed. Differences in the development of the infraorbital artery subdivisions can, in some cases, be related to the types of dentition or the lack of dentition exhibited by each group of living reptiles.

The cranial venous system of *Eocaptorhinus* is in most cases more difficult to trace than is the arterial system. Orbital and palatal sinuses appear to have been an important part of the system. In *Eocaptorhinus* the main system of venous drainage from the palate was apparently anteriorly into the rostral sinus thence posterodorsally through the orbitonasal vein to the orbital sinus. In lizards the flow is completely reversed. The orbitonasal vein has been lost. Venous blood travels anteroventrally into the rostral sinus thence posteriorly into the lateral palatal sinus from which it drains dorsally through the suborbital fenestra by way of the pterygoid vein. *Sphenodon* exhibits a pattern intermediate between these two extremes, a small orbitonasal vein draining the dorsal snout region posteriorly into the orbital sinus and a small pterygoid vein draining through the lateral palatal foramen into the vena capitis lateralis. The palatal venous system in pelycosaurs was much different, apparently having drained posteroventrally through the external mandibular vein.

The cranial circulatory system of the captorhinid *Eocaptorhinus* is of a generally primitive form thought to be common to many, if not all, captorhinomorphs. It is suspected, but by no means sure, that a connection between the posterolateral extremity of the lateral palatal sinus and the external mandibular vein was a primitive reptilian characteristic that has been lost in modern reptiles but that has been greatly expanded in mammals. The dorsal M. adductor mandibulae externus superficialis branch of the external mandibular vein in many modern turtles may be a remnant of this primitive link. The development of a prominent anterior circulation from the palatal sinuses to the rostral sinus, thence through the snout to the orbit is an advanced characteristic of captorhinomorphs and their modern descendents. Pelycosaurs had a very different cranial circulatory system even at the time of their first appearance in the fossil record. While it is probable that the pelycosaurian cranial circulatory system developed from a pattern similar to that of non-synapsid reptiles, the separation must have occurred long before the first appearance of captorhinomorphs with their specialized palatal venous drainage.

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CRANIAL MUSCULATURE
OF
PRIMITIVE CAPTORHINID REPTILES

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ABSTRACT

Superbly preserved remains of the captorhinomorph reptile *Eocaptorhinus laticeps* from the Lower Permian Wellington formation (Wolfcampian) of northcentral Oklahoma have revealed well developed muscle origin and insertion scars. Reconstruction of the mandibular adductor musculature on the basis of these scars on skull elements reveals that captorhinomorphs possessed a typically reptilian tripartite M. adductor mandibulae. The M. adductor mandibulae posterior was a small simple muscle. The M. adductor mandibulae externus was extremely complex with three subdivisions, the partes superficialis, media, and profunda, each of which was further subdivided. The M. adductor mandibulae internus was divided into two bipartite muscles, the M. pseudotemporalis and the M. pterygoideus. There was a well developed tripartite M. constrictor dorsalis group.

These muscles were essential components in a primitively metakinetic skull, some serving as skull roof elevators during mandibular depression and others serving as parts of either a kinetic inertial or a static pressure system during mandibular adduction. This primitive metakinetic condition developed concomitantly with the attainment of a very small size, and hence small terrestrial insectivore feeding mode, that must have been necessary for the development of the amniote egg.

FIGURES

Fig. 1. *Eocaptorhinus laticeps.* Skull. Reconstruction.

Fig. 2. Geometry and anatomy of muscle origins and insertions.

Fig. 3. Muscle Tension-Elongation Curve.

Fig. 4. Primary divisions of the M. adductor mandibulae.

Fig. 5. *Eocaptorhinus laticeps.* Skull roof in ventral aspect showing regions of muscle origin.

Fig. 6. *Eocaptorhinus laticeps.* Braincase showing regions of muscle origin.

Fig. 7. *Eocaptorhinus laticeps.* Regions of muscle origin and insertion.

Fig. 8. *Eocaptorhinus laticeps.* Head in lateral aspect showing the M. adductor mandibulae externus superficialis and its divisions, the M. levator anguli oris and the M. retractor anguli oris. Reconstruction.

Fig. 9. *Eocaptorhinus laticeps.* Head in lateral aspect showing the M. adductor mandibulae externus superficialis with the M. levator anguli oris and M. retractor anguli aris removed. Reconstruction.

Fig. 10. *Eocaptorhinus laticeps.* Head in dorsal aspect showing the mandibular adductor musculature. Reconstruction.

Fig. 11. *Eocaptorhinus laticeps.* Head in dorsal aspect. Reconstruction.

Fig. 12. *Eocaptorhinus laticeps.* Head in lateral aspect showing the M. adductor mandibulae externus medius segments. Reconstruction.

Fig. 13. *Eocaptorhinus laticeps,* Palatal complex showing regions of muscle origin.

Fig. 14. *Eocaptorhinus laticeps.* Head in lateral aspect showing the M. pseudotemporalis superficialis, M. intramandibularis, and the M. adductor mandibulae posterior. Reconstruction.

Fig. 15. *Eocaptorhinus laticeps.* Head in ventral aspect showing the M. pterygoideus. Reconstruction.

THE ADDUCTOR MANDIBULAE MUSCULATURE OF A PRIMITIVE CAPTORHINID REPTILE

Introduction

The early Permian terrestrial deposits of the southern United States have produced a large fauna of primitive reptiles. It is from these deposits that the well known mammal-like or synapsid reptiles, *Dimetrodon*, a sphenacodonid pelycosaur, has been collected (Romer and Price, 1940). From here also have come many specimens of the Order Captorhinomorpha, often considered to be the most primitive group of true reptiles. Most of these belong to the Family Captorhinidae. Two species, *Captorhinus aguti* of early Leonardian age (Fox and Bowman, 1966) and the slightly earlier *Eocaptorhinus laticeps* of late Wolfcampian age (Heaton, 1975, 1978) (Fig. 1) have been exhaustively studied. *Eocaptorhinus* is known from a large collection of superbly preserved specimens from the Wellington Formation of northcentral Oklahoma (see Heaton, 1975, 1978, for specimen numbers, descriptions, and locality data) that reveal muscle attachment "scars". Since little information on the adductor jaw musculature of primitive captorhinomorphs is available in the literature, a reconstruction of the pattern present in *Eocaptorhinus laticeps*, the earliest adequately known captorhinomorph is presented. Although Fox (1964) has attempted to reconstruct the musculature of a captorhinomorph, *Captorhinus aguti*, in detail unfortunately this was done on the basis of an assumed mammalian muscle arrangement (Barghusen, 1968, 1973).

Detailed studies of the adductor musculature of primitive Paleozoic reptiles are rare. Because of the superb reconstructions of the skull of the early Permian sphenacodontid pelycosaur *Dimetrodon*, presented by Romer

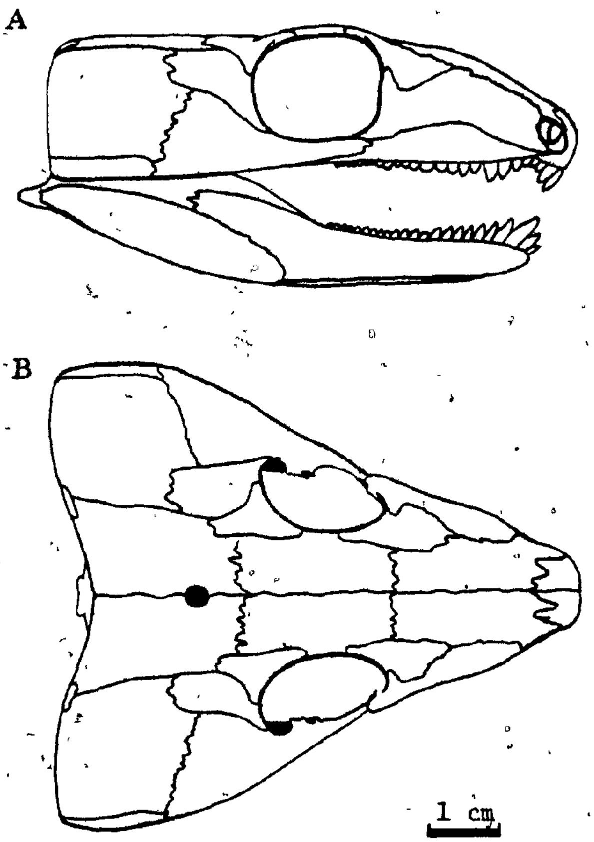


Figure 1. *Eocaptorhinus laticeps*. Skull. a) Lateral aspect. b) Dorsal aspect. Reconstruction. Natural size.

and Price (1940), and the availability of numerous well preserved and prepared specimens, most studies have concentrated upon this genus (Watson, 1948; Parrington, 1955; Fox, 1964; Barghusen, 1968, 1973).

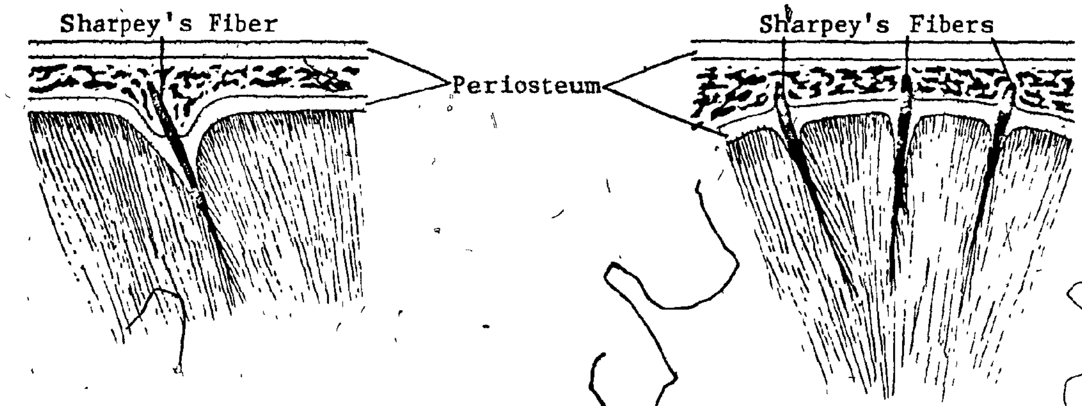
Any attempt at reconstructing the cranial soft anatomy of fossil reptiles presupposes an extensive knowledge of the cranial anatomy of modern reptiles and, to a lesser extent, of modern amphibians and mammals. In the past, such reconstructions have been erratic in quality since few paleontologists have had a sufficiently good understanding of anatomy to permit good reconstructions to be made and anatomists have generally been uninterested in fossil forms. Only Barghusen (1968, 1972, 1973) and Ostrom (1961, 1964, 1966) have achieved any notable success in this field.

The literature on modern reptilian cranial anatomy is also limited. Much of the published information is old and often inaccurate or grossly over-simplified. Much was acquired by means of careful dissection. Since the general decline of comparative anatomy since the 1930's, little has been published beyond reviews of the older literature. Comparative vertebrate anatomy is making a noticeable reappearance as a necessary tool in vertebrate paleontology though most research has been confined to mammals. As a result, relevant anatomical knowledge had to be acquired first hand by means of extensive dissections of modern forms. In this study one or more specimens of the following modern reptiles has been dissected: *Pseudemys concinna* (Chelonia: Testudinidae), *Pseudemys scripta* (Chelonia: Testudinidae), *Ctenosaura pectinata* (Lacertilia: Iguanidae), *Gekko gecko* (Lacertilia: Gekkonidae), *Iguana iguana* (Lacertilia: Iguanidae), *Phrynosoma cornutum* (Lacertilia: Iguanidae), *Tupinambis nigropunctatus* (Lacertilia: Teiidae), and *Varanus bengalensis* (Lacertilia: Varanidae). In addition, a number of modern amphibians was examined in concert with

Robert B. Holmes of McGill University: *Ambystoma maculatum* (Urodela: Ambystomatideae), *Amphiuma tridactylium* (Urodela: Amphiumidae), *Ascaphus truei* (Anura: Ascaphidae), *Cryptobranchus alleganiensis* (Urodela: Cryptobranchidae), *Hynobius retardatus* (Urodela: Hynobiidae), *Necturus maculosus* (Urodela: Proteidae), *Rana pipiens* (Anura: Ranidae), *Siren lacertina* (Urodela: Sirenidae), and *Xenopus* sp. (Anura: Pipidae).

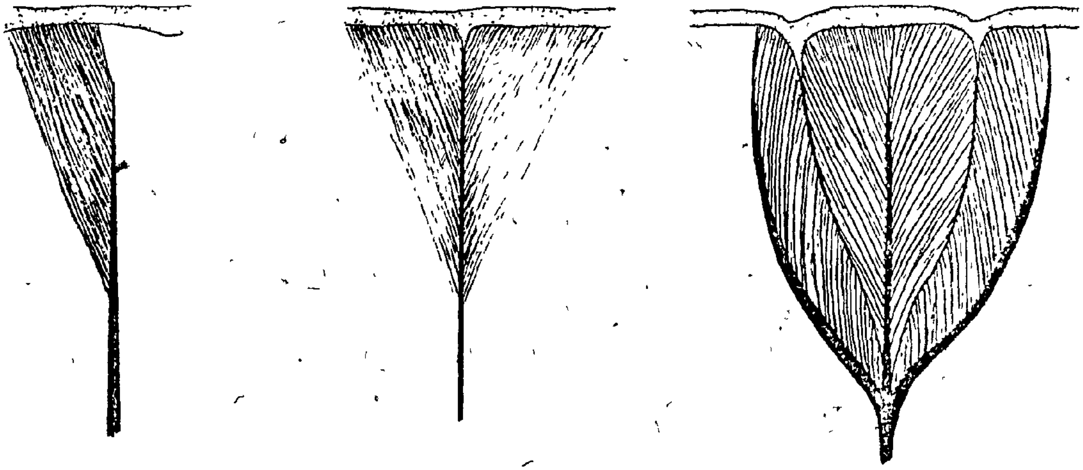
The mandibular adductor musculature of modern reptiles is basically similar even though the three major groups, the chelonians (turtles and tortoises), lepidosaurs (rhynchocephalians, lizards, and snakes) and crocodilians have evolved separately for at least 200 million years. Both chelonians and crocodilians have become highly specialized in their skull structure and modes of feeding with a consequent change in emphasis in the development of some segments of the adductor musculature. Rhynchocephalians (*Sphenodon*) and many lizards, although specialized in the development of two pairs of temporal fenestrae in the skull roof and cheek have a generally similar skull size and construction, and for the most part, have retained a primitive reptilian insectivorous feeding mode and hence have retained the primitive pattern of reptilian muscle segment development. Since the muscle development in these primitive lepidosaurians is less specialized than in either turtles, which superficially resemble the unfenestrate skulled captorhinomorph reptiles, or in crocodilians, comparison with relatively unspecialized lizards such as *Iguana* and *Tupinambis* and the primitive, sphenodontid rhynchocephalian *Sphenodon* is stressed.

Barghusen (1973) has given an excellent rationale for identifying the regions of muscle origin and insertion in fossil reptiles. Some explanation and amplification of his criteria do seem appropriate. The major criterion he used was the presence of attachment "scars" that were to be considered homologous by reason of similar placement in both the fossil and living reptiles. Attachment "scar" is a frequently used but poorly defined term. Basically there are two methods of anchoring muscles to bones. These are fleshy connections and tendinous connections (Edwards, 1946). All bone surfaces are sheathed in a layer of dense mesenchymal connective tissue, the periosteum, the deep layer of which produces osteoblasts that deposit thin, dense layers of lamellar bone. This applies to both dermal and perichondral or periosteal bone although their exact process of formation is slightly different (Romer, 1970). The periosteum is bound to the lamellar bone by short bundles of collagenous fibers known as Sharpey's fibers (Edwards, 1946; Frazzetta, 1968) (Fig. 2). As Frazzetta noted, greater stresses are placed on the periosteum by forces associated with perpendicular or near perpendicular muscle attachments than by sub-tangential attachments. In regions where the periosteum is heavily stressed, additional clusters of Sharpey's fibers are produced so that fossils, from which all organic components been removed, show an increased degree of microscopic pitting where the Sharpey's fibers have been lost. Many perpendicular muscle attachments cover large areas in order to dissipate stress across the periosteum. This type of broad attachment is always fleshy although it may be supported by minor tendons. Slightly dished or excavated areas of perpendicular muscle attachment are typical because the external boundaries of the muscle produce slightly greater stresses and hence greater degrees of ossification (Edwards, 1946). In these cases, the rims often show weak concentrations of Sharpey's fibers pits. In regions of inclined or nearly tangential muscle attachment, extreme shear loads



Muscle origin from ridge
ridge supported tendon

Tendon supported fleshy
muscle origin



Unipinnate muscle
insertion onto
tendon

Bipinnate muscle
insertion onto
tendon

Multipinnate muscle
insertion onto
tendon

Figure 2. Geometry and anatomy of muscle origins and insertions.

may be placed on the periosteum. In these cases, a collagenous extension of the periosteum, a tendon, is normally formed in whose base are embedded many bundles of Sharpey's fibers, around which additional fleshy attachments, resulting from a pinnate attachment of the muscles to the tendon, are developed. The increased numbers of Sharpey's fibers give the ridge a heavily pitted surface and, in areas of extreme stress, this, as well as differential ossification at the base of the tendon produces, a heavily gnarled region. These bony evidences of muscle or tendon attachment are the scars to which reference is often made.

Each muscle fiber has a single fixed length at which it will come to rest if unexcited and if not subjected to any external applied compressive or tension forces. This is known as the resting fiber length and is usually considered to represent 100 percent elongation of the muscle fiber (Fig. 3). Each division and subdivision of a muscle mass may, and usually does, reach its resting fiber length at a different point in the mechanical cycle through which the skeletal elements, to which it is attached, pass. When the muscle fiber is stimulated, it may contract as much as 30 percent of its resting fiber length, but as it does so, the active tension in the activated muscle decreases from a maximum at the resting fiber length to zero at its point of maximum contraction (Zierler, 1961). This has two consequences in jaw adduction. First, a unitary adductor mass, while being strong at one position, would be relatively weaker at other points in the jaw adduction cycle. Obviously a jaw adductor muscle mass with numerous divisions and subdivisions that reach their resting fiber lengths sequentially and, thus, exert a constant force throughout the adduction cycle, is a

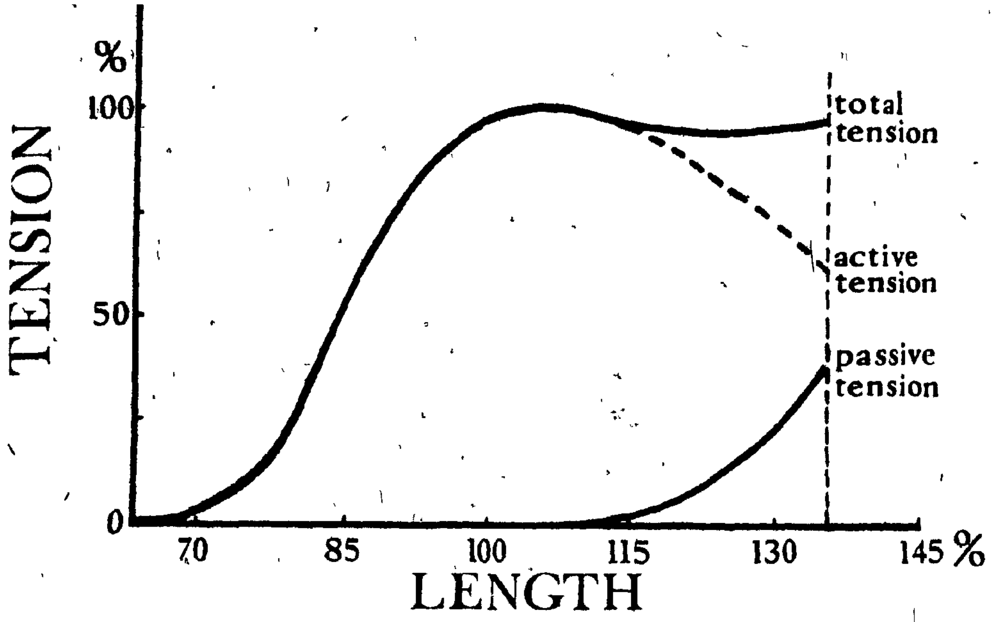


Figure 3. Muscle Tension-Elongation Curve (after Zierler 1961).

distinct advantage. Second, forms with complex subdivided jaw adductor musculature primitively show a proportionately larger cross-sectional area of muscle fiber in order to maintain adequate strength throughout the cycle. Animals with simpler jaw adductor muscles usually have proportionately smaller cross-sectional areas of these muscles unless some structure or mechanism, such as the coronoid process in nammals (DeMar and Barghusen, 1973) or the extremely mobile cranial kinesis in gekkonid lizards, has been developed to overcome the problems of a single, or at least, extremely limited number of positions of maximum active tension.

Muscles can be stretched passively beyond their resting fiber length by the application of an external force, usually the contraction of another muscle, on the mechanical system. Passive tension increases geometrically with elastic elongation to about 130 to 140 percent of the resting fiber length before inelastic elongation of some muscle fiber components begins and passive tension rapidly decreases (Zierler, 1961). Haines (1932, 1934) has shown that striated skeletal muscle adapts its maximum elastic fiber length under passive tension to the greatest degree of physical excursion in the mechanical system of which it is a part. An increase in tendon length at the expense of muscle fiber length is typical in systems where physical movement has been restricted. In all such cases, the tendon adjusts the maximum elastic fiber length under passive tension to about 130 to 140 percent of the resting fiber length. Barghusen (1968), in his reconstructions of the jaw adductor musculature in the sphenacodont pelycosaur, *Dimetrodon*, used a factor of 132.6 percent elongation as the maximum fiber length. This figure was derived from an idealized, generalized tension-elongation graph based on results obtained by Zierler (1961) using human skeletal muscle (Fig. 3). Haines (1934) does not quote any figures for elongation as Barghusen (1968) has implied. Because of the numerous generalizations necessary to determine the point of maximum elastic muscle fiber elongation under passive tension, a figure of 132.6 percent is thought to represent spurious accuracy, especially when an extrapolation of experimental values obtained from human skeletal muscle is applied to primitive reptilian musculature. The figure is believed to range between 130 and 140 percent but may be as high as 140 to 150 percent as suggested by Gans (1966) and Reisz (1972) but surely does not reach the 200 percent suggested by some authors.

Frequently the term 'resting fiber length' has been misinterpreted, especially when being discussed in relation to the jaw adductor musculature of modern reptiles. It has usually been assumed that all mandibular adductor muscle fibers reach their resting fiber lengths when the mandible is adducted. This rapidly leads to the assumption that primitive reptiles were limited in the degree to which the mandible could be depressed (Reisz, 1972) or that the muscle fibers of primitive reptiles could accommodate greater elastic elongation. Examination of the skull and jaw adductor musculature of modern reptiles reveals a similar apparent discrepancy between the maximum observed degree of mandibular depression and the assumed resting fiber lengths. In fact, what has happened is that the original assumption that all muscles are at their resting fiber length when the mandible is adducted is incorrect. Only one muscle segment need be maintained at its resting fiber length to keep the mouth closed without the need for continuous active tension in the muscle mass. This segment, usually the most posterior of the mandibular adductor divisions in order to remain as close to the jaw articulation (fulcrum) as possible, so as to decrease the degree of angular excursion and thus muscle fiber elongation, keeps most other muscles in slight compression thus leading to the commonly observed passive bulging of the jaw adductor musculature when the mouth is closed. Muscles having origins or insertions, or both, at some distance from the jaw articulation reach their own resting fiber lengths when the mandible is depressed to a specific degree for each individual muscle segment.

The re-constructions of the mandibular adductor musculature in *Eocaptorhinus laticeps* have been made to represent, as closely as possible, the actual appearance of the animal as if being dissected today. All nerves and blood vessels have been reconstructed in their appropriate positions. Certain liberties have been made in the re-construction of the skin and the pupil of the eye for the sake of artistic continuity. A pattern of large non-imbricate scales was selected to cover the lightly sculptured lateral snout elements since this is similar to the form of scalation to be observed in at least some members of most groups of modern reptiles where relatively large size and thick bone and skin are present. Reconstruction of the skin covering the heavily sculptured cheek and skull roof is more difficult. It is felt that this region was probably covered by many small, non-imbricate epidermal scales, one scale possibly corresponding in size roughly to each sculpture pit. Large plaque-like scales or small imbricate scales would appear to be inappropriate for a region of heavy pit-and-ridge sculpturing. The general appearance of the scalation would probably resemble that of a larger teiid lizard such as *Tupinambis* if the scales were simple and unadorned. An elliptical pupil of the eye similar to that seen in crocodilians and many lizards is illustrated although there is, of course, no concrete evidence to support or contradict this aspect of the reconstruction. All other features of the re-constructions are supported by one or more pieces of corroborating evidence.

M. ADDUCTOR MANDIBULAE OF *EOCAPTORHINUS LATICEPS*

The older, and some of the newer, literature has often considered the jaw adductor musculature to be an undifferentiated or bipartite muscle usually referred to as the M. temporalis (Meckel, 1812-33; Cuvier, 1836-46; Stannius, 1856; Owen, 1866; Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; von Teutleben, 1874; Hoffman, 1879-90; Shufelt, 1890; Edgeworth, 1907; Lubosch, 1933) in accord with the presumed homologies with the mammalian, and in particular the human temporal musculature, or the M. capitimandibularis (Hoffman, 1879-90; Bradley, 1903; Adams, 1919; Fox, 1964) in comparative anatomy (origin-insertion) terminology. Luther (1914) and Lubosch (1914) were the first to describe a tripartite separation of the adductor musculature of amphibians based on the position of the divisions of this musculature based on the position of the divisions of this musculature relative to the maxillary and mandibular rami of the trigeminal nerve which innervates these muscles. This system was applied to a discussion of the homologies of the jaw adductor muscles of modern reptiles by Lakjer (1926). It is his scheme that has generally been accepted by anatomists and most paleontologists (Schumacher, 1953, 1953-54, 1954-55a, b, 1956a, b, c, 1973a, b; Oelrich, 1956; Haas, 1960, 1973; Ostrom, 1961, 1964, 1966; Barghusen, 1968, 1972, 1973; Gomes, 1974). Many paleontologists have used other terms, or presumed homologies, when trying to reconstruct the adductor musculature of fossil reptiles, often using mammalian musculature and terminology for comparison (Watson, 1948; Parrington, 1955; Olson, 1961; Crompton, 1963; Crompton and Hotton, 1967; Fox, 1964) with the result that much of the available data are badly confused. As Lakjer (1926) pointed out, all modern reptiles possess a tripartite jaw adductor formed of the M. adductor mandibulae posterior that lies posteroventral to the mandibular division of the trigeminal nerve (V_3), the M. adductor mandibulae externus that lies anterolateral to the mandibular ramus (V_3) and ventrolateral to the maxillary ramus (V_2) of the trigeminal nerve, and the M. adductor mandibulae internus anteromedial to the maxillary ramus (V_2) of the trigeminal nerve and lateral to the pterygoid and epipterygoid (Fig. 4). Also innervated through a separate ramus and medial to the pterygoid and epipterygoid are the small muscles of the M. constrictor dorsalis group.

The M. adductor mandibulae divisions are themselves further subdivided. While it is usually recognized that the M. adductor mandibulae internus is divided into discrete M. pseudotemporalis and M. pterygoideus segments in all modern reptiles and most amphibians, this is not the case with the other two divisions. The M. adductor mandibulae posterior is a small muscle in reptiles with a single homogeneous origin and insertion. In contrast to amphibians, it is seldom sub-divided. The adductor mandibulae externus on the other hand, is divided into three distinct parts (except in the Gekkota), the partes superficialis, media, and profunda. Only Ostrom (1961, 1964, 1966) has taken these divisions into account when reconstructing the jaw musculature of fossil forms.

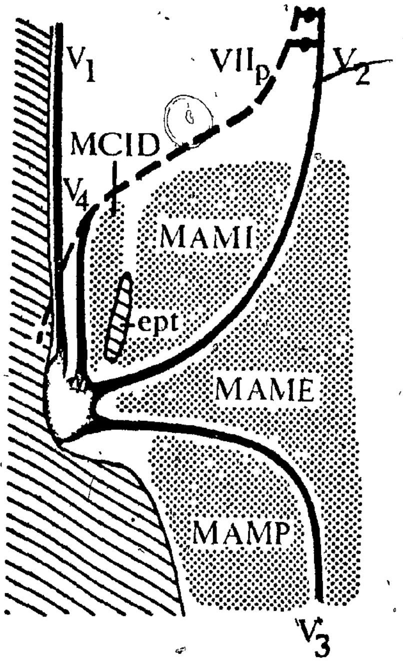


Figure 4. Primary divisions of the M. adductor mandibulae of a typical reptile in frontal section.

The three parts of the M. adductor mandibulae externus have fixed positions relative to the bones of the skull roof, the mandibular tendons (basal aponeurosis), and certain nerves and blood vessels, especially arteries. If these landmarks can be identified in fossil forms, then the parts of the M. adductor mandibulae externus, and even some of their sub-divisions, can be identified. The heavily ossified skulls of the primitive reptiles with their large areas of origin and insertion are ideally suited for this type of reconstruction (Figs. 5, 6, and 7). These attachment areas must be identified and muscles joining them be reconstructed with due regard for the positions of all nerves and blood vessels.

M. adductor mandibulae externus (MAME)

The M. adductor mandibulae externus of most modern reptiles is divided into three segments, the partes superficialis, media, and profunda. The only known exceptions to this rule are the gekkonid lizards which have, as a consequence of the loss of the temporal arches, reduced the degree of segmentation of the M. adductor mandibulae externus. Attempts to reconstruct the adductor musculature of fossil reptiles based largely on a gekkonid model (Crompton and Hotton, 1967) are severely handicapped by the difficulty in determining which characteristics are primitive and which specialized in this family. Snakes have a tripartite M. adductor mandibulae externus but, in the absence of an insertional basal aponeurosis, the homologies of the parts cannot be established with confidence. For this reason, snakes and their jaw adductor musculature are not discussed in detail. Large relatively primitive lizards (iguanids and teiids), the sole surviving rhynchocephalian *Sphenodon punctatus*, cryptodire turtles, and crocodilians have formed

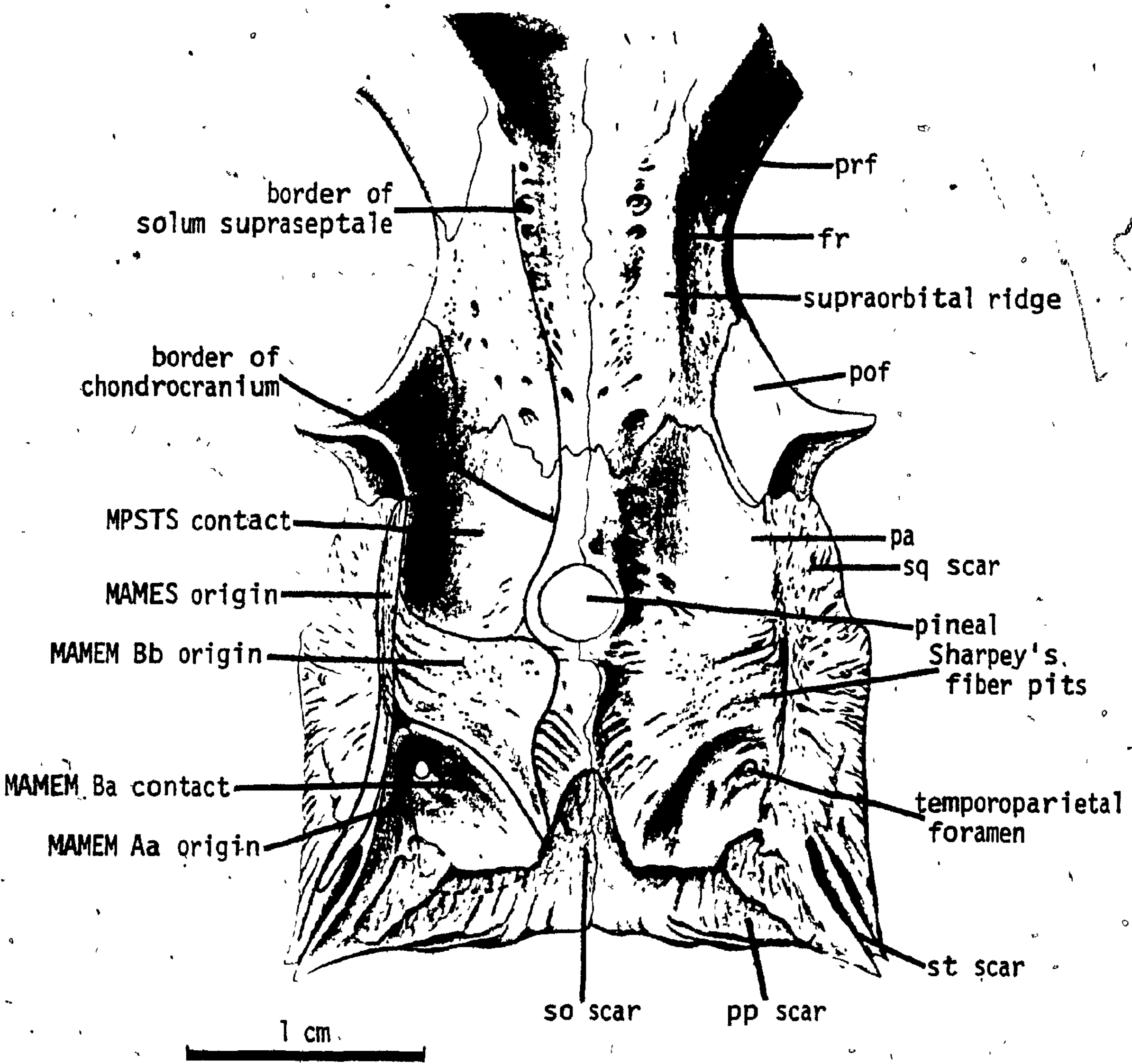


Figure 5. *Eocaptorhinus laticeps*. Skull roof in ventral aspect showing regions of muscle origin.

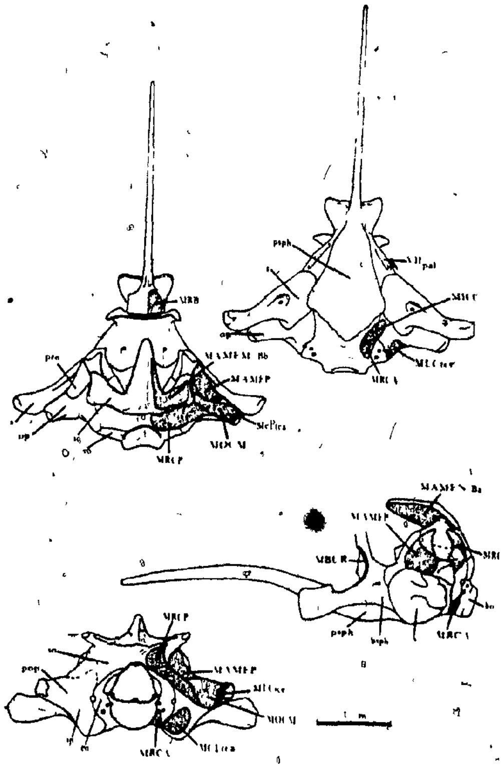


Figure 6. *Eocaptorhinus laticeps*. Braincase showing regions of muscle origin. a) Dorsal aspect. b) Ventral aspect. c) Lateral aspect. d) Occipital aspect.

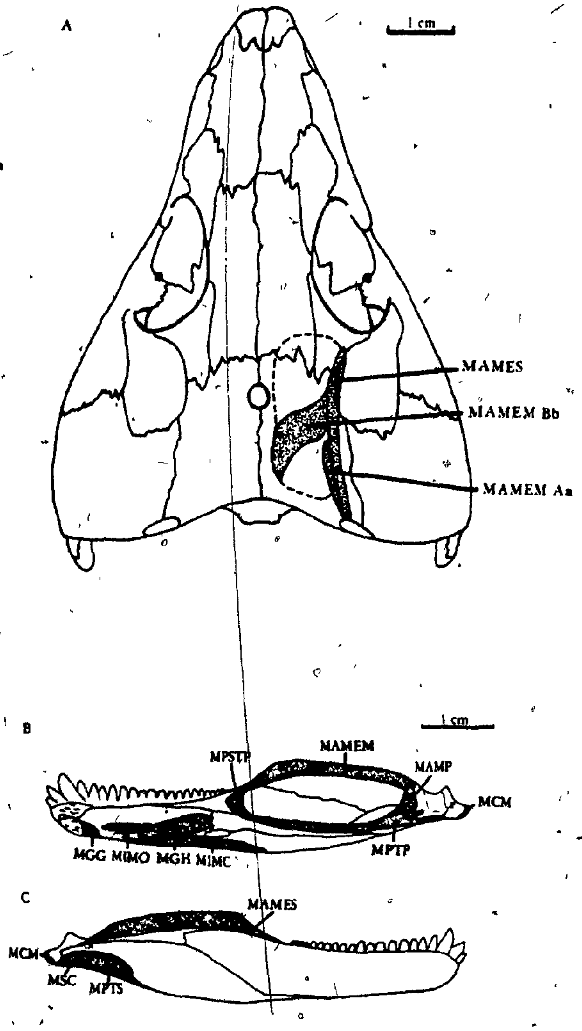


Figure 7. *Eocaptorhinus laticeps.* Regions of muscle origin and insertion. a) Skull transparency in dorsal aspect. b) Mandible in medial aspect. c) mandible in lateral aspect.

the basis from which an understanding of the origins, insertions, related structures, and functions of the adductor mandibulae musculature of reptiles has been developed.

M. adductor mandibulae externus superficialis

The pars superficialis of the M. adductor mandibulae externus originates from the medial surfaces of the posterior process of the postfrontal and the anterior process of the squamosal, which form the dorsal temporal arch, in *Sphenodon*. The origin is similar in most lizards except in forms, such as the gekkonid lizards, in which the dorsal temporal bar has been lost (Lakjer, 1926; Brock, 1938; Haas, 1973). In crocodilians, because of the extensive modificiation of the braincase and posterior region of the adductor chamber, the pars superficialis originates from the ventral surface of the quadratojugal and the lateral surface of the quadrate (Schumacher, 1973a). In most turtles, which retain a primitive unfenestrated (anapsid) skull, albeit with variable degrees of posterior and ventral emargination of the skull roof and cheek respectively, the pars superficialis originates from the postfrontal and variously, in addition, from the parietal; from the dorsal surface of the quadrate, the squamosal, and the prootic; from the opisthotic and the basisphenoid; or, where temporal emargination is extreme, from the temporal fascia (Schumacher, 1973a). The M. adductor mandibulae externus superficialis is typically bounded laterally by the temporal fascia (Decksehne of Poglayen-Neuwall, 1953, 1954) and medially by the external tendon (Sehnenplatte).

In all cases, and in fact by definition (Lakjer, 1926), the M. adductor mandibulae externus superficialis lies lateral to all divisions of the basal aponeurosis ("Bodenaponeurosis" of authors) or tendon sheet.

In *Sphenodon* and lizards the pars superficialis is divided into a medial segment (M. adductor mandibulae externus 1b of Lakjer, 1926) that is apparently homologous with the entire pars superficialis of crocodilians and most turtles, and a lateral division (M. adductor mandibulae externus 1a of Lakjer, 1926) composed of a single muscle sheet in lizards, the M. retractor anguli oris (often called the M. levator anguli oris even though it pulls posterodorsally or retracts rather than pulling dorsally or elevating) and of two elements in *Sphenodon*, a posterior sheet-like M. retractor anguli oris and a narrow, vertical anterior M. levator anguli oris (Lakjer, 1926; Haas, 1973). In modern turtles and crocodilians, the anteroposterior width of the M. adductor mandibulae externus superficialis is short relative to the length of the skull, thus the angular acceleration of the mandible is high as would be expected in forms requiring a quick snapping action in order to catch fast moving prey (crocodiles) or to shear food into small portions using a sharp keratinous beak (turtles). A short lever arm such as this results in a limited degree of circumferential elongation about its distal end. In turtles and crocodilians, the rictal plates are shallow since a minimum of folded skin is required in the Mundplatte system to accommodate elongation of the adductor musculature. Although the heavily keratinized skin of reptiles is much less elastic than is the skin of mammals it does still allow some stretching. Thus, as the ventral cheek margin becomes emarginated in both advanced turtles and crocodiles, and the pars superficialis insertion migrates ventrally on the lateral surface of the mandible in some turtles, more and more of the elongation of the skin overlying the adductor musculature can be accommodated by simple stretching rather than by a much more complex plaited Mundplatte system. In *Sphenodon* and lizards, the M. adductor mandibulae externus superficialis is wide relative to the length of the skull, being approximately 45 to 50% in *Sphenodon,* about 40% in *Iguana* in contrast to only 25 to 30% in *Pseudemys* and *Alligator.* The degree of elongation of the adductor muscle at the posterior angle of the mouth in modern lepidosaurs is great enough that a deeply folded Mundplatte system with well developed lateral and medial rictal plates is necessary in order to compensate for this elongation. If selection has been toward a relatively slow speed but high power adductor system such as this, a separate muscle slip from the pars superficialis must surely also have been developed in order to operate the deep Mundplatte efficiently. This is especially true for any form with a complete, unemmarginated ventral cheek border since there is no leeway to allow skin stretching to assume a significant role in the accommodation of M. adductor mandibulae elongation. If this aspect is considered, the Mundplatte-M. retractor anguli oris system of lizards must have been well developed before the loss of the lower temporal bar, otherwise skin stretch and temporal emargination would have become the principal means of accommodating adductor lengthening. In *Eocaptorhinus laticeps,* the width of the M. adductor mandibulae externus superficialis represented between 45 and 50% of the total skull length or about the same as in *Sphenodon.* Likewise a straight ventral cheek margin and failure of the pars superficialis to extend below it when the jaws were adducted, suggest the presence of a deep Mundplatte in *Eocaptorhinus* that most probably was supported by a separate lateral slip of the pars superficialis (Fig. 8). In lizards, where a large anterodorsally projecting quadrate has restricted the posterior portion of the adductor region, the

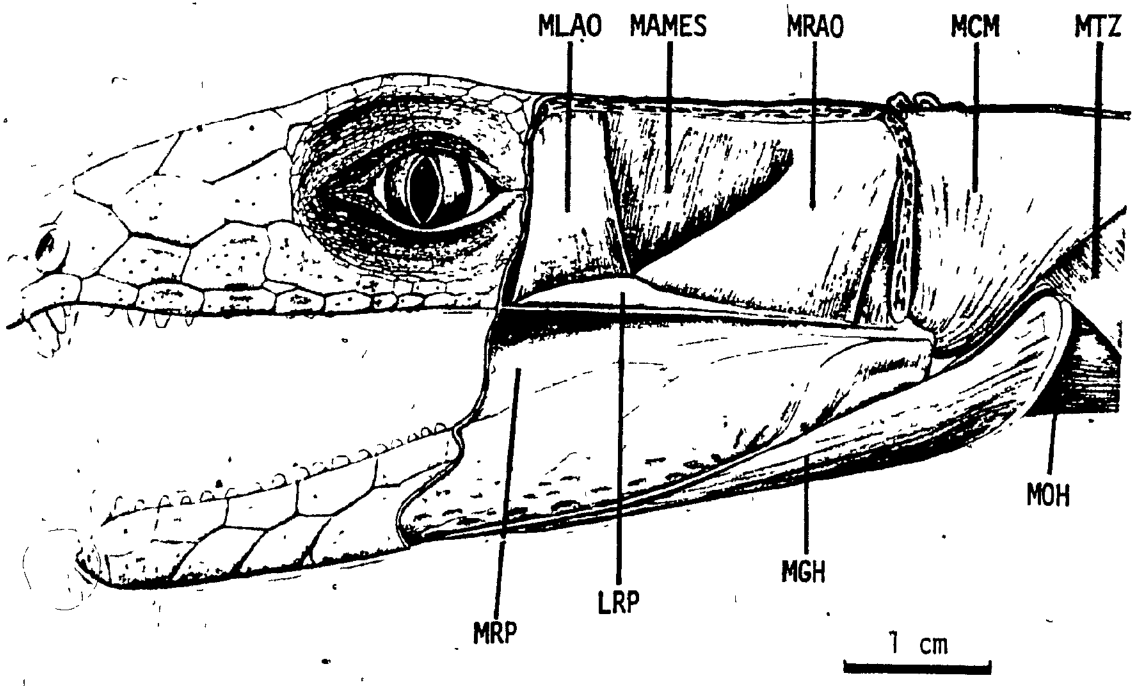


Figure 8. *Eocaptorhinus laticeps*. Head in lateral aspect showing the M. adductor mandibulae externus superficialis and its lateral divisions, the M. levator anguli oris and M. retractor anguli oris. Reconstruction.

M. retractor anguli oris origin has migrated anteriorly with this muscle becoming the only one inserting on the medial rictal plate. *Eocaptorhinus,* like *Sphenodon,* has a small dorsally oriented quadrate that does not impinge upon the adductor chamber. As a result, two separate muscles, a dorsally oriented M. levator anguli oris and a posterodorsally directed M. retractor anguli oris appear to satisfy the mechanical requirements of rictal plate support in *Eocaptorhinus* as they do in *Sphenodon.*

In turtles and crocodiles, tendons are not normally associated with the origin of the M. adductor mandibulae externus superficialis. *Sphenodon* and lizards, on the other hand, have numerous auxillary tendons. The posterodorsomedial surface of the pars superficialis is typically covered by a prominent aponeurosis (Decksehne of Ingeborg Poglayen-Neuwall, 1953, 1954). Muscle fibers of the main segment of the pars superficialis parallel this tendinous sheath but do not, for the most part, originate from it. The muscle fibers extend ventrolaterally then ventrally to form a pinnate insertion onto the lateral surface of the dorsomedially inclined lateral sheet of the external tendon (Binnensehne of Ingeborg Poglayen-Neuwall, 1953, 1954) of the basal aponeurosis (Bodenaponeurosis) and onto the lateral surface of the coronoid and surangular ventral to the tendon. The presence and position of these tendons has been shown to be remarkably consistent amongst lizards (Gomes, 1972).

The internal skull roof of *Eocaptorhinus* exhibits a heavily gnarled and pitted ridge extending along the lateral edge of the ventral surface of the parietal just medial to the suture with the postorbital and squamosal (Fig. 5). This is interpreted as the site of attachment, as revealed by the many prominent Sharpey's fiber pits, of a well developed dorsal external aponeurosis. There is no evidence of heavy tendinous insertions on the squamosal just lateral to the parietal, but scattered light pitting indicates the presence of a fleshy origin of a thin, wide muscle lateral to the tendon which is interpreted here as the main segment of the M. adductor mandibulae externus superficialis (Figs. 9 and 10). It appears that, as the superior temporal fenestra developed in diapsid reptiles, and the lateral extent of the parietal shrank, the origins of the M. adductor mandibulae externus superficialis migrated laterally onto the squamosal.

The insertion of the M. adductor mandibulae externus superficialis in *Eocaptorhinus* appears to have been essentially similar to that of modern reptiles. It is believed that a well developed basal aponeurosis existed as in all modern reptiles with the exception of snakes. Pinnate insertion onto the lateral surface of the most lateral element of the external tendon of this system would be typical (Fig. 11). An extensive region of the lateral surface of the surangular is covered with a uniform field of tiny Sharpey's fiber pits that indicate a broad region of fleshy attachment of the pars superficialis to the bone. The coronoid did not extend dorsally in *Eocaptorhinus* as it does in *Sphenodon* and modern lizards, and so did not receive muscle fibers laterally as part of a fleshy insertion. It appears that in *Eocaptorhinus* and the later, larger captorhinids, that the pars superficialis became an exceptionally large muscle developing the very heavily ossified pars superficialis origin ridge on the parietal and the greatly increased degree of "cheek swelling" characteristic of these forms.

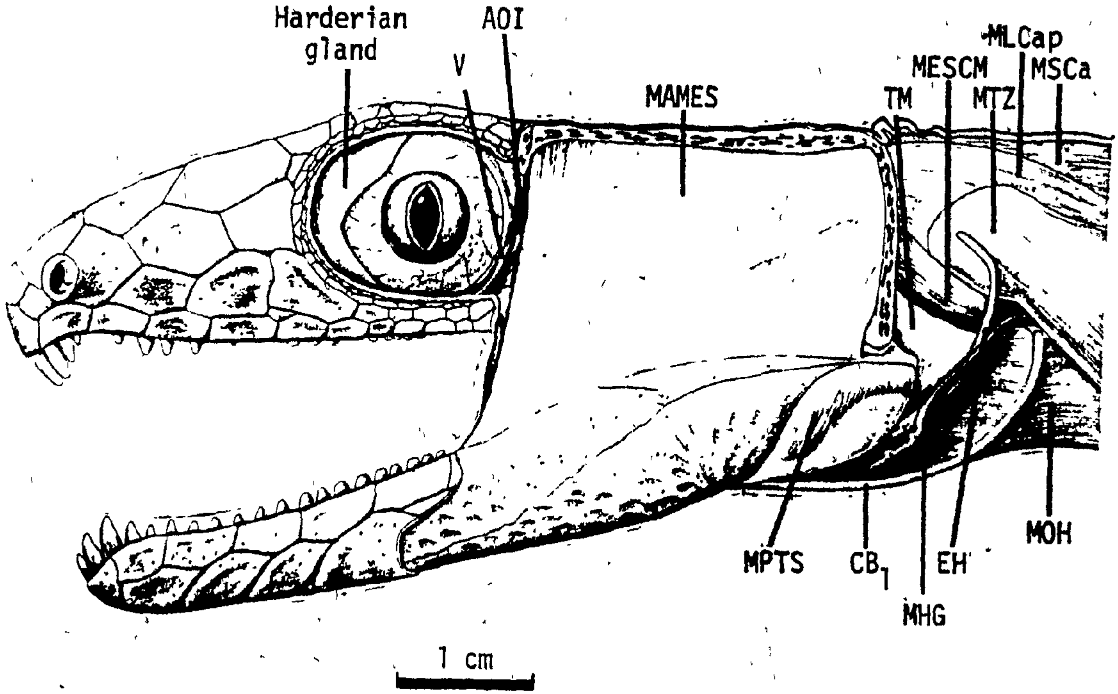


Figure 9. *Eocaptorhinus laticeps*. Head in lateral aspect showing the M. adductor mandibulae externus superficialis with its M. levator anguli oris and M. retractor anguli oris removed. Reconstruction.

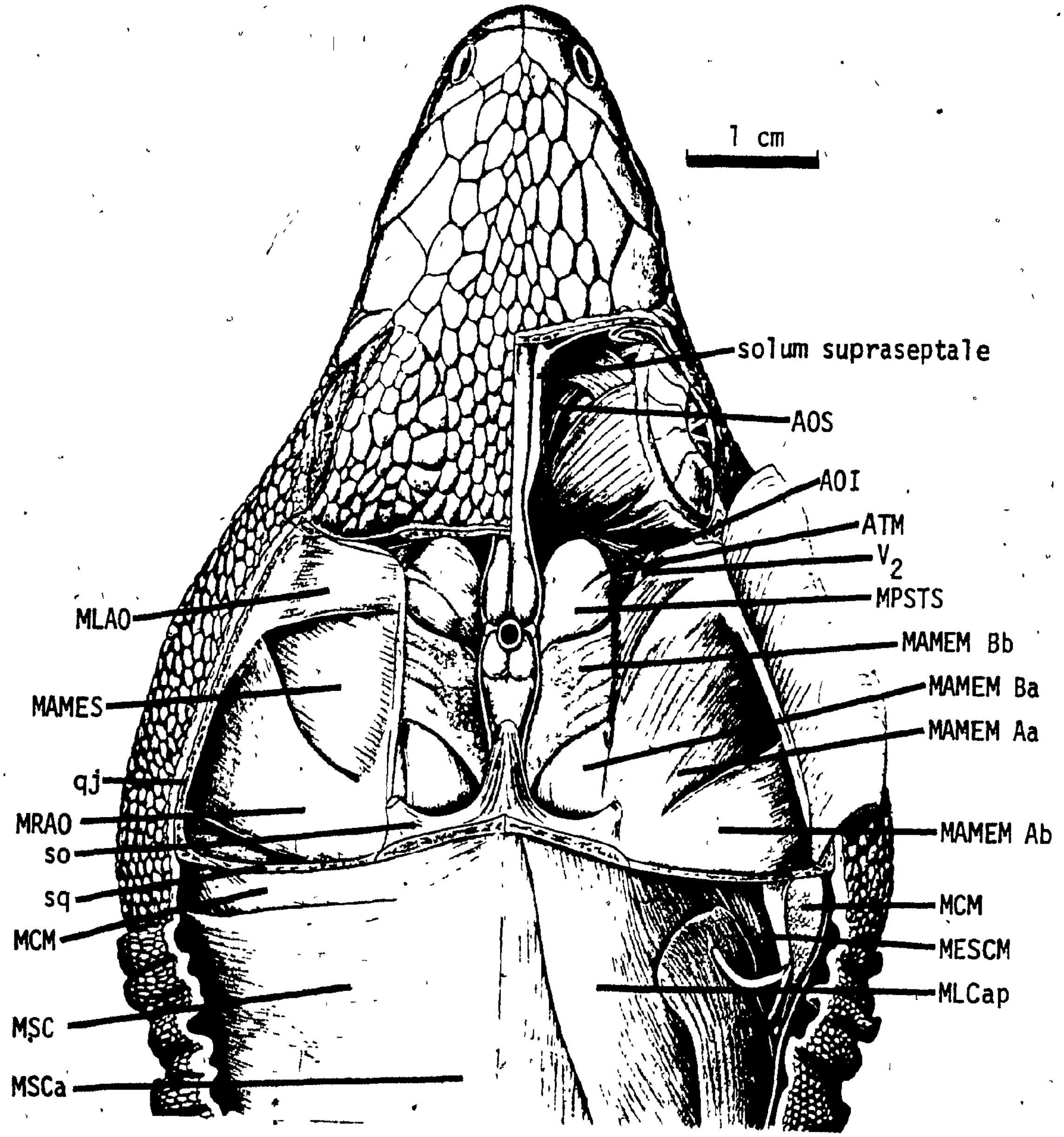


Figure 10. *Eocaptorhinus laticeps*. Head in dorsal aspect showing the mandibular adductor musculature. Reconstruction.

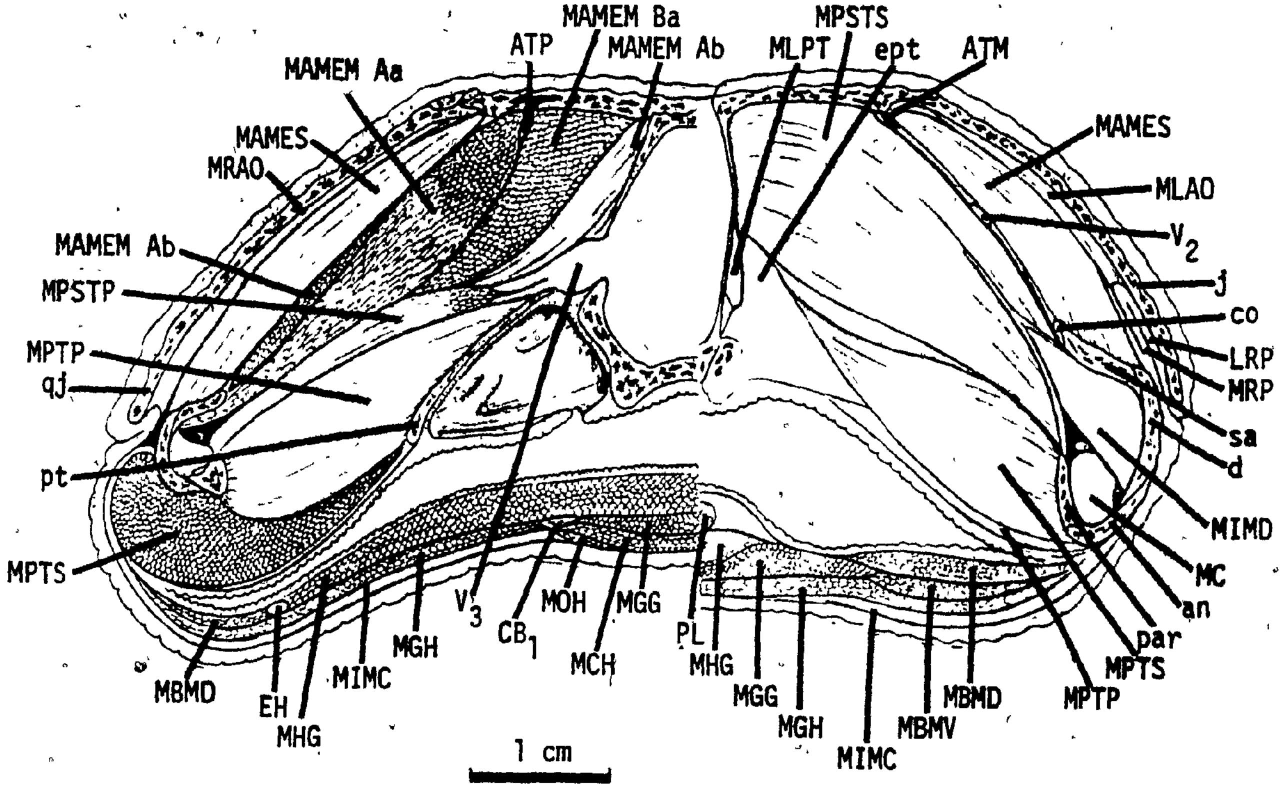


Figure 11. *Eocaptorhinus laticeps.* Head in cross-section. A) Transverse plane through incisura prootica. B) Transverse plane through sella turcica. Reconstruction.

In order to produce an accurate re-construction of the adductor musculature of *Eocaptorhinus*, the degree of maximum mandibular depression must be determined. In modern iguanid lizards, the maximum angle of mandibular depression has been observed to be approximately 40 degrees. In those forms such as the varanid lizards, with highly kinetic skulls, a greater angle can be attained. Since the length of the adductor chamber is about 50 percent of the skull length in *Eocaptorhinus* rather than only about 30 percent in iguanid lizards and since cranial kinesis was less well developed in *Eocaptorhinus*, the maximum angle of mandibular depression selected for the reconstruction as appropriate, is less than for iguanid lizards. This is in general accord with figures obtained by using the longest potential muscle fiber length of the M. adductor mandibulae externus superficialis extending from the most anterior fleshy origin to the most anterior fleshy insertion at the base of the basal aponeurosis. With a sheet-like, relatively straight-fibered muscle such as the pars superficialis, compression beyond the point of maximum contraction is not likely to have been significant. This is in marked contrast to the apparent condition in a curved-fiber muscle such as the M. pseudotemporalis superficialis where considerable passive compression apparently existed when the mandible was adducted. If, as is expected, the M. adductor mandibulae externus superficialis is fully contracted but not compressed when the mouth is closed, then 40 to 45 percent elongation from the contracted position (30 to 35 percent resting fiber length) to the resting fiber length position reveals a mandibular depression angle of about 15 degrees (as illustrated). An additional elongation under passive tension by about 30 to 40 percent of the resting fiber length or 85 to 100 percent of the maximum contracted length produces a maximum angle of mandibular depression of about 30 degrees. Considerable confusion has existed in the literature regarding muscle fiber elongation and hence the degree of maximum mandibular depression, much of it resulting from the confusion between the resting fiber length and the minimum contracted length. Elongation and active contraction of about 30 to 40 percent of the resting fiber length is possible from the resting fiber length position. Elongation but not active contraction, of up to 85 percent to 100 percent of the minimum contracted length or 60 to 80 percent of the resting fiber length is possible from the fully contracted, but not compressed position.

M. adductor mandibulae externus medius

The pars media is the most strongly developed segment of the M. adductor mandibulae externus in *Sphenodon* and lizards. It is also large in turtles and crocodilians where it is usually somewhat smaller than the pars profunda. The pars media of *Sphenodon* and lizards is roughly divided into two segments by the temporal artery which penetrates its posterior end. Each of these segments, designated M. adductor mandibulae externus medius A laterally and B medially is further sub-divided, by small intermediate tendons, into as many as four smaller divisions each (Lakjer, 1926; Haas, 1973). The lateral or A segment originates from the squamosal and opisthotic while the medial or B segment originates from the parietal and supraoccipital. The pars media inserts onto the anteromedial surface of the external tendon of the basal aponeurosis and onto subsidiary medial tendinous laminae of the external tendon (Lakjer, 1926; Haas, 1973).

The extensive modification of the braincase and pterygoids associated with the development of the secondary palate and cranial akinesis in turtles and crocodilians has altered the structure of the posterodorsal border of the adductor chamber and, thus, extensively modified the origins of the M. adductor mandibulae externus medius. In many turtles, and also in crocodiles, extensive and often extreme specialization of the cranial arterial system in the adductor region has prevented the establishment of exact homologies between sub-divisions of the M. adductor mandibulae externus medius. The insertion of the pars media is similar to that seen in *Sphenodon* and lizards.

The M. adductor mandibulae externus medius appears to have been the largest and most powerful muscle in the head of *Eocaptorhinus laticeps* as well as the most complex (Fig. 12). Two-thirds of the ventral surface of the parietal, which roofs the adductor chamber, is devoted to the origin or accommodation of the pars media. Two distinct regions are visible, an anterior trapezoidal area with five posteromedially directed low ridges marked by many Sharpey's fiber pits and a smaller, posterior parabolic excavation with lateral pitting and a large anterior temporoparietal foramen. The pars media evidently was divided into two units separated by the temporal artery. A short dorsal branch of this artery is believed to have entered the temporoparietal foramen. This artery and its associated foramen establish the position of the division between the lateral and medial divisions of the pars media (M. add. mand. ext. 2A and 2B of Lakjer, 1926). These two main muscular divisions do not conform to the two topographic divisions. The lateral division of the pars media consisted of at least one and possibly two thin slips. The primary lateral slip (pars media Aa) originated tendinously from the lateral rim of the posterior parabolic depression lateral to the temporoparietal foramen. It is apparent from the marked line of Sharpey's

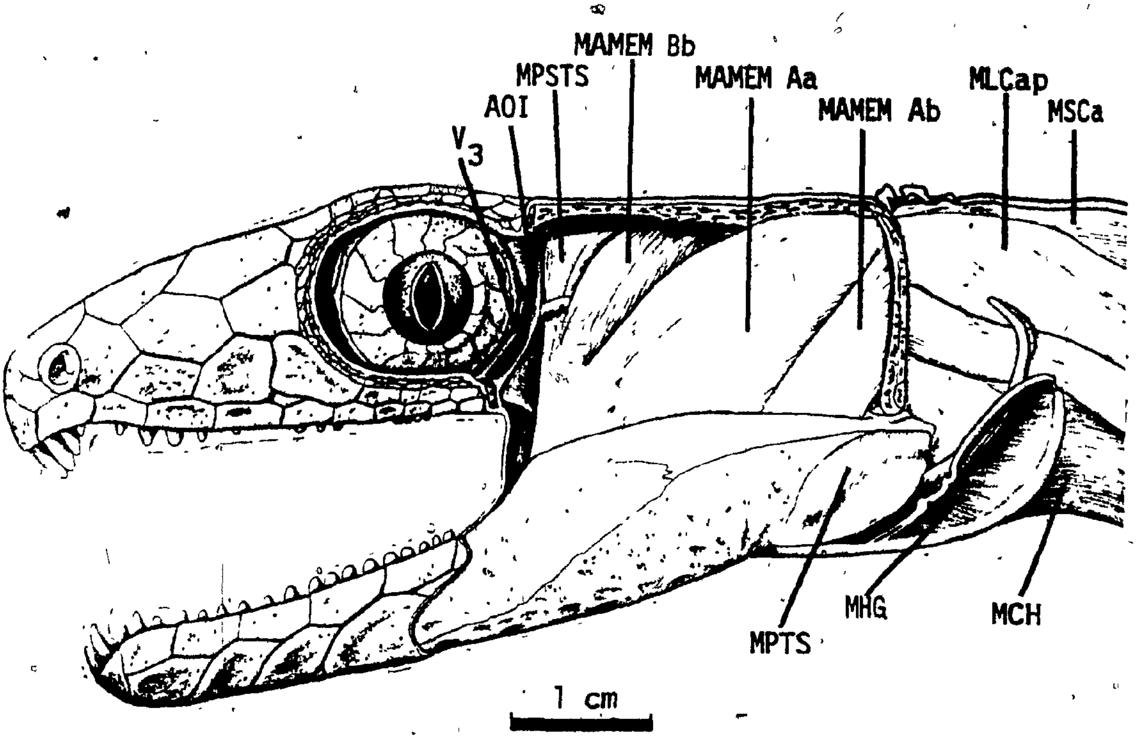


Figure 12. *Eocaptorhinus laticeps*. Head in lateral aspect showing the M. adductor mandibulae externus medius segments. Reconstruction.

fiber pits that the muscle fibers were oriented posterodorsolaterally to originate on the medial surface of the posterior end of the external aponeurosis. The tendon attachment ridge, although heavily pitted, is not gnarled, thus implying that adduction forces decreased posteriorly toward the jaw articulation as moment theory predicts. This long, thin, wide muscle apparently extended anteroventrally to insert pinnately onto the lateral surface of a medial sheet of the external tendon. The medial tendon sheet has been reconstructed in order to compensate for a small fiber length shortfall that occurs when the assumed 30% maximum contraction calculation is employed and to keep muscle fiber orientations in line. The pattern resulting from this procedure is similar to that seen in *Sphenodon*, *Iguana* (Lakjer, 1926), *Tupinambis*, and many other lizards.

A thin, narrow superficial slip of the lateral division of the pars media (pars media Ab) has been reconstructed with a fleshy origin on the anterior surface of the occipital flanges of the quadrate and squamosal and an insertion medial to the lateral sheet and lateral to the medial sheet of the posterior end of the external tendon (Fig. 12). This is the most weakly documented to the adductor muscles. Its presence is proposed as a filler between the straight fibered pars media Aa immediately medial to it and the arched pars superficialis laterally. In addition, it has the shortest muscle fiber length of any adductor muscle inserting on the mandibulae, thus reducing passive stretch considerably and acting as a major stabilizer of the jaw articulation. Such a muscle (illustrated as M. add. mand. ext. 2c but described as M. add. mand. ext. 2d by Haas, 1973) is present in *Sphenodon* as well as in many lizards including *Iguana* and *Tupinambis*.

The medial segment of the M. adductor mandibulae externus medius (pars media B) was divided into two units. The posterior unit (pars media Ba) is judged to have filled the parabolic depression of the parietal medial to the temporal artery and the lateral segment of the pars media (pars media Aa) (Figs. 5, 7, and 10). The depression in the parietal is smoothly surfaced without Sharpey's fiber pitting. It appears that the pars media Ba was not attached to the ventral surface of the parietal but rather had a fleshy origin on the heavily pitted anterior surface of the lateral ascending process of the supraoccipital. This muscle apparently bulged dorsally against the skull roof when the mandible was adducted but was probably separated from it slightly when the mandible was depressed. Because the parabolic depression was formed principally as a means of accommodation for slight swelling of the pars media Aa, which originated along its lateral margin, and the pars media Ba medially, there are no preserved osseous reflections of the interface between these two muscle segments except for the diagnostic temporoparietal foramen.

The pars media Ba, judging by its relationship to the anteromedial pars media Bb, inserted onto the lateral surface of a slightly more medial segment of the medial lamina of the external tendon anteromedial to the pars media Aa. The pars media Bb inserted onto the lateral surface of this tendinous sheet. Physical evidence of these sub-divisions of the external tendon is absent. They are reconstructed here to provide as simple a means as possible of accommodating the insertion of muscles, with definable sub-divisions, while maintaining necessary muscle fiber orientations and functionally viable mechanical arrangements of the mandible and adductor musculature. All modern turtles and lepidosaurs (except snakes) possess a multilaminate external tendon in the basal aponeurosis system. Although this appears to be a primitive characteristic, it is not possible to homologize all of the laminae amongst modern reptiles.

A large trapezoidal scar on the ventral surface of the parietal anteromedial to the previously determined position of the body of the M. adductor mandibulae externus media Ba and posterolateral to the M. pseudotemporalis superficialis and braincase is believed to have been the area from which the M. adductor mandibulae externus media Bb originated. Five or six tendinous laminae apparently were anchored to a similar number of low ridges that bear major Sharpey's fiber pit concentrations. Together they trended posteromedially through the bulk of the pars media Bb parallel to the pars media Ba-Bb and pars media Bb-M. pseudotemporalis superficialis interfaces. These supplementary tendons formed the base of a multipinnate lateral origin of the pars media Bb. In addition, the posteromedial region of the pars media Bb apparently had a strong fleshy origin from the lateral face of the median ascending process of the supraoccipital and the cartilaginous taenia marginalis dorsal to the incisura prootica. Anteroventrally, the pars media Bb is believed to have inserted onto the medial surface of the pars media Ba insertional lamina of the external tendon of the basal aponeurosis.

As in *Sphenodon* and lizards, the pars media is thought to have been, with the M. pseudotemporalis superficialis, the major power adductor with the pars media Ba and Bb almost equal in cross-sectional area and together constituting the majority of the pars media mass. In both turtles and crocodilians, the pars media is relatively smaller with less well defined sub-divisions. These simplifications are apparently derived, not primitive, conditions related to the extreme specializations of the braincases and temporal artery circulation systems in these two groups and to the emphasis on the pars profunda in turtles and the M. pseudotemporalis and M. pterygoideus in crocodilians as the major power adductors.

M. adductor mandibulae externus profundus

The structure of the M. adductor mandibulae externus profunda is similar in those modern reptiles where the braincases are not excluded from the adductor chamber by the pterygoid and quadrate and which possess large post-temporal fenestrae. The pars profunda of *Sphenodon* and lizards has a fleshy double headed origin on the lateral surface of the supraoccipital (or in some cases the overlapping parietal) and on the dorsolateral surface of the prootic (Lakjer, 1926; Haas, 1973). Turtles have increased the area of pars profunda origin on the supraoccipital, prootic, and opisthotic and dorsomedially onto the descending lamina of the parietal and laterally onto the quadrate. The pars profunda is the major mandibular adductor in turtles. Crocodilians, although having arisen from forms with a primitive braincase-adductor musculature arrangement similar to that believed to have been present in *Eocaptorhinus*, have modified the braincase so extensively that the pars profunda origin is now excluded from the braincase entirely. This has led to considerable disagreement as to the exact homologies of the pars profunda (Lakjer, 1926; Anderson, 1936; Ivo Poglayen-Neuwall, 1953; Iordansky, 1964; Schumacher, 1973a) and its frequent confusion with the M. adductor mandibulae posterior.

The M. adductor mandibulae externus profundus of *Eocaptorhinus laticeps* has been re-constructed with a double headed fleshy origin on the lateral surface of the supraoccipital and on the anterodorsal surface of the prootic and opisthotic (Fig. 6) much as in *Sphenodon* which it resembles in the structure of the adductor chamber. The pars profunda apparently arched anteriorly over the dorsal margin of the quadrate ramus of the pterygoid posterior to the epipterygoid thence ventrally to its insertion posteriorly onto the medial surface of the pars media insertional lamina of the external tendon. It lay ventral and medial to the pars media, medial to the pars superficialis and lateral to the M. pseudotemporalis. When contracted, it probably bulged posteriorly into the post-temporal fenestra.

M. adductor mandibulae posterior

All modern reptiles possess a relatively simple M. adductor mandibulae posterior. It typically originates from the quadrate and inserts onto the posterior region of the medial insertional lamina of the external tendon (Vorderfahne of Ingeborg Poglayen-Neuwall, 1953) (Lakjer, 1926; Haas, 1973; Schumacher, 1973a). In *Sphenodon* this muscle is often inclined (Haas, 1973) as it is in *Tupinambis*. In the latter, however, a massive anterior M. adductor mandibulae posterior pars intermandibularis has developed to aid in adduction. This is a unique and presumably specialized characteristic in this large lizard (Ingeborg Poglayen-Neuwall, 1954; Haas, 1973).

The M. adductor mandibulae posterior in *Eocaptorhinus* is believed to have been a small, simple muscle that occupied the posteromedial portion of the adductor chamber (Figs. 13 and 14). It appears to have had a broad fleshy origin on the lateral face of the pterygoid lamella and anterior surface of the occipital flange of the quadrate as far ventrally as the mandibular articulation (Fig. 13). Its dorsolateral surface was probably covered by a thin medial lamina of the external

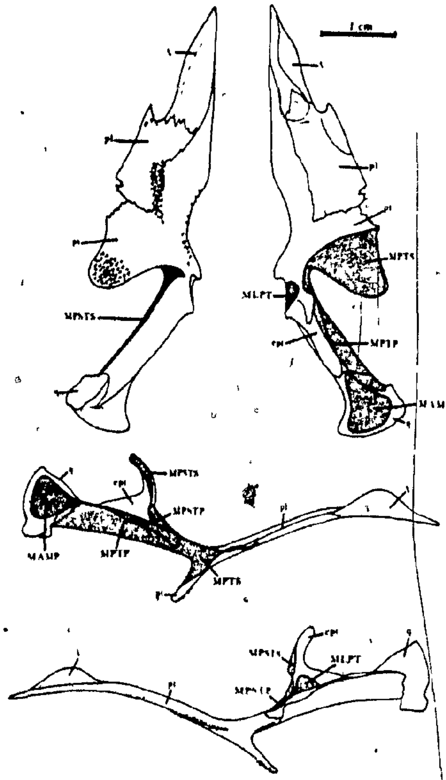


Figure 13. *Eocaptorhinus laticeps*. Palatal complex showing regions of muscle origin. a) Dorsal aspect. b) Ventral aspect. c) Medial aspect. d) Lateral aspect.

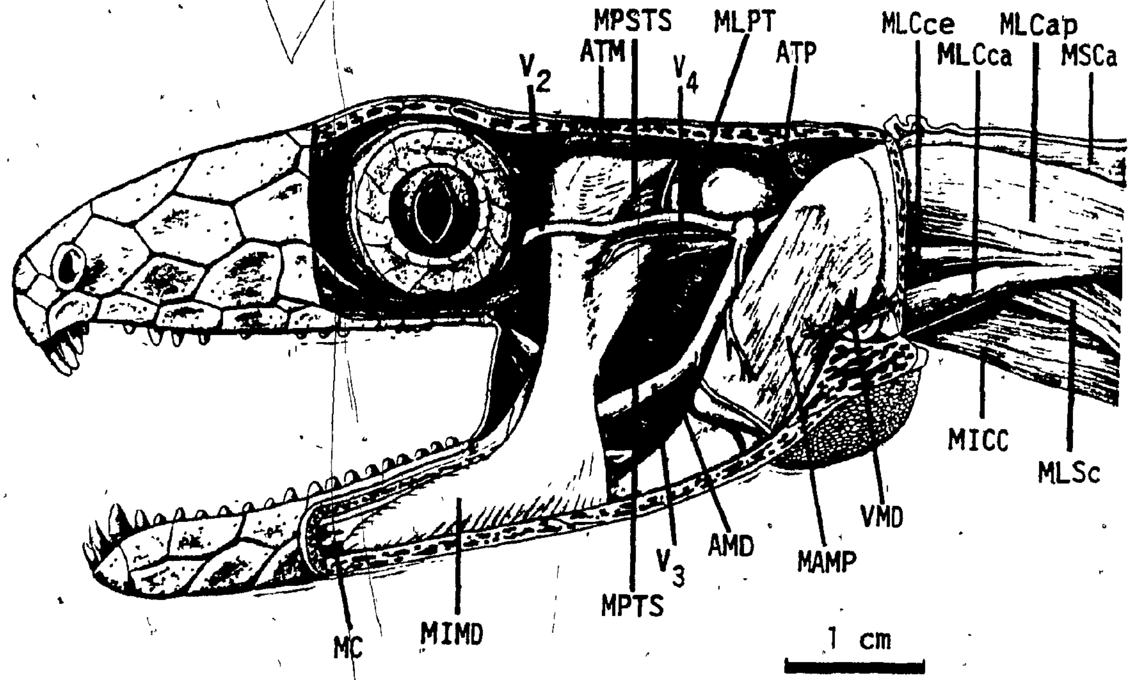


Figure 14. *Eocaptorhinus laticeps*. Head in lateral aspect showing M. pseudotemporalis superficialis, M. intramandibularis, and M. adductor mandibulae posterior. Reconstruction.

aponeurosis which separated the muscle from the M. adductor mandibulae externus medius Aa and Ab.

The M. adductor mandibulae posterior appears to have extended laterally into the posterior half of the adductor fossa where it inserted onto the dorsolateral surface of the articular and, apparently, the Meckelian cartilage. Shorter medial fibers formed a pinnate insertion onto the lateral surface of the posterior segment of the internal tendon of the basal aponeurosis. There is little difference between the origins, insertions, and structure of this muscle as it is believed to have existed in *Eocaptorhinus* and as it is in modern reptiles.

M. adductor mandibulae internus

The M. adductor mandibulae internus of modern reptiles is always divided into at least two major segments which, by tradition, have been given full recognition as separate muscles. These are the M. pseudotemporalis and the M. pterygoideus. In addition, crocodilians and many turtles have a well developed M. intramandibularis.

M. pseudotemporalis

The M. pseudotemporalis is a muscle of quite varied size in modern reptiles. It is well developed in *Sphenodon* and most lizards where it is typically sub-divided into superficial and deep segments. Gekkonid, pygopodid, and possibly xantusiid lizards, as well as snakes, are exceptions since they have a secondarily reduced, undifferentiated M. pseudotemporalis as do turtles. Crocodiles have a large single M. pseudotemporalis that appears to be homologous with the pars superficialis of *Sphenodon* and most lizards.

M. pseudotemporalis superficialis

In *Sphenodon*, most lizards, and crocodiles, the dorsal temporal fenestra is partially or entirely filled with the large mass of the M. pseudotemporalis superficialis. The pars superficialis in *Sphenodon* originates from the posterior surface of the postorbital and from the medial, descending flange of the parietal so as to fill the anterior portion of the dorsal temporal fenestra ahead of the slightly larger M. adductor mandibulae externus medius. The M. pseudotemporalis of most primitive lizards, with the exception of the gekkotan families (Gekkonidae, Pygopodidae, Xantusiidae), fills the anterior portion of the dorsal temporal fenestra as in *Sphenodon*, and similarly originates from the medial, descending flange of the parietal. In more advanced lizard families (Lacertidae, Teiidae, Varanidae), the M. pseudotemporalis superficialis is larger than the M. adductor mandibulae externus medius and often fills the dorsal temporal fenestra. In these forms, the M. pseudotemporalis superficialis may originate from the anterior surface of the supratemporal as well as from the lateral surface of the medial, descending flange of the parietal (Lakjer, 1926; Haas, 1973). *Sphenodon* and lizards with poorly developed mesokinesis, such as the Iguanidae and larger members of the Teiidae have a well developed separation between the partes superficialis and profunda of the M. pseudotemporalis.

The M. pseudotemporalis of crocodilians is essentially similar to the pars superficialis of *Sphenodon* and most lizards and appears to be its homologue. The M. pseudotemporalis of crocodiles originates from the parietal, supraoccipital, squamosal, and alisphenoid. This increase in the latitude of origination sites is related to the great modification of the braincase and apparently related decrease in the size of the dorsal temporal fenestra in modern crocodiles.

The M. pseudotemporalis of turtles is a relatively small muscle that originates from the lateral surface of the descending process of the parietal and partly from the anterior surface of the prootic. The muscle is normally undivided, except in the case of the chelydrid *Macroclemys* and the testudinid *Platysternon*. The origin of the M. pseudotemporalis superficialis in *Sphenodon* and most lizards and seemingly can be interpreted as being its homologue. The pars profunda is, thus, interpreted as being absent in most forms. Barghusen (1973) considered a small, undifferentiated M. pseudotemporalis, such as is seen in most turtles, to be characteristic of all primitive reptiles. He believed this muscle to be the homologue of the pars profunda of *Sphenodon* and lizards and that the pars superficialis in these latter forms is a specialization in which the M. pseudotemporalis has invaded the dorsal temporal fenestra. It is believed that this is not the case, however, for the origin is more like that of the M. pseudotemporalis superficialis of lizards and *Sphenodon* on the parietal rather than on the epipterygoid as is the origin of the M. pseudotemporalis profundus in these animals.

The M. pseudotemporalis superficialis is typically pyramidal in form with one apex directed ventrally to form a bipinnate attachment onto the M. pseudotemporalis tendon. In turtles the bulk of the muscle is reduced compared with that of *Sphenodon* and most lizards, but the insertion onto the M. pseudotemporalis tendon is the same. The M. pseudotemporalis of turtles does not insert onto the medial surface of the coronoid and internal tendon and, thus, does not satisfy Lakjer's (1926) criteria for identification as a pars profunda of the M. pseudotemporalis. The M. pseudotemporalis of gekkotan lizards does satisfy these conditions and is, thus, identified as a pars profunda (Lakjer, 1926; Haas, 1973). In *Sphenodon*, non-gekkotan lizards, crocodilians, and turtles, the M. pseudotemporalis tendon, onto which the M. pseudotemporalis superficialis inserts, is a major segment of the basal aponeurosis (Bodenaponeurosis of Ingeborg Poglayen-Neuwall, 1953; Barghusen, 1973). It is located at the anterior extremity of the adductor fossa and is formed by the union of the laminae of both the external and internal tendons. In both crocodilians and turtles, the M. pseudotemporalis tendon serves additionally as a dorsal insertion of a M. intramandibularis.

Well preserved specimens of *Eocaptorhinus* seem to provide solid evidence that a differentiated M. pseudotemporalis with a large pars superficialis was a primitive characteristic of captorhinids and probably all primitive reptiles. The M. pseudotemporalis of *Eocaptorhinus* appears to have been a bipartite muscle that lay anterolateral to the pterygoid and epipterygoid. There was no medial, descending flange of the parietal ensheathing the dorsolateral portion of the chondrocranium on which the M. pseudotemporalis superficialis could originate, as there is in *Sphenodon*, many lizards, and turtles. The M. pseudotemporalis superficialis is believed to have been a large muscle that had a fleshy origin on the lateral surface of the chondrocranium (taenia parietalis) including the sellar processes and pila antotica (Figs. 6 and 14). Posteriorly some fibers appear, also, to have originated from the anterior surface of the columella of the epipterygoid. A smoothly rounded depression on the ventral surface of the parietal anterior to the M. adductor mandibulae externus medius Bb origin scar indicates that none of the M. pseudotemporalis superficialis muscle fibers originated from this bone (Fig. 5). It is apparent that, when the mandible was adducted, the pars superficialis bulged against the ventral surface of the parietal but that a slight amount of space may have separated muscle and bone when the mandible was depressed.

The M. pseudotemporalis superficialis tapered rapidly ventrally as indicated by the apparent position and configuration of the M. adductor mandibulae externus medius Bb. The M. pseudotemporalis superficialis concentrated its fibers onto a narrow lateral M. pseudotemporalis lamina of the internal tendon, at its junction with the external tendon, that extended into the anterior end of the adductor fossa (Figs. 11 and 14). This tendon, while part of the system attaching the muscle to the medial rim of the adductor chamber, also served to link the M. pseudotemporalis with the M. intramandibularis.

M. pseudotemporalis profundus

Sphenodon and all modern lizards possess a pars profunda of the M. pseudotemporalis. In gekkonid and pygopodid lizards, the pars profunda is the only segment of the M. pseudotemporalis remaining (Lakjer, 1926; Haas, 1973). As Haas noted, the absence of the pars superficialis in these forms and in snakes seems to be correlated with the loss of the upper temporal bar in these animals. The presence of only a pars profunda does not appear to be a primitive feature as Barghusen (1973) believed. In *Sphenodon*, the M. pseudotemporalis profundus is variable in its development. It normally has an anterior head originating from the ventrolateral surface of the medial, descending flange of the parietal and the anterior edge of the epipterygoid. There is also a smaller posterior head that originates from the posteromedial edge of the expanded dorsal extremity of the epipterygoid. This expanded dorsal extremity lies between the two heads of the pars profunda (Haas, 1973). The muscle fibers from both of these heads converge to form a broad, fleshy insertion onto the medial surface of the coronoid and the anterior extremity of the articular. There is no prearticular in *Sphenodon*. Since the epipterygoid of lizards (except chamaeleonids where the epipterygoid has been lost) is more slender than that of *Sphenodon*, the M. pseudotemporalis profundus is not separated by it into distinct anterior and posterior heads. Instead, the pars profunda normally has a fleshy origin on the lateral surface of the cartilaginous and membranous braincase anterior and just posterior to the epipterygoid, which it surrounds laterally, and may extend posteriorly to originate from the anteromedial edge of the prootic. As in *Sphenodon*, the M. pseudotemporalis profundus of lizards inserts onto the medial surface of the coronoid and, occasionally, the anterior end of the prearticular. A distinct, identifiable M. pseudotemporalis profundus has not been recognized in either crocodilians or in turtles (Lakjer, 1926; Schumacher, 1973).

The M. pseudotemporalis profundus of *Eocaptorhinus* is believed to have originated on the lateral surface of the chondrocranium, ventromedial to the origin of the pars superficialis, and also to the dorsal and lateral surfaces of the epipterygoid (Fig. 13) since there was neither a median descending flange of the parietal nor a large alar process of the prootic from which to originate as there is in *Sphenodon* and most none gekkotan lizards. The large anterolateral crest on the columella of the epipterygoid is thought to have divided the pars profunda into distinct anterior and posterior heads. Anterior to the crest, the epipterygoid is heavily scarred by a diffuse pattern of Sharpey's fiber pits that are indicative of a broad, steeply inclined fleshy origin, possibly with minor tendon support. The majority of the anterior head is believed to have originated from the lateral surface of the chondrocranium. The posterior surface of the columella of the epipterygoid bears some Sharpey's fiber pitting, but it is not as extensive as on the anterolateral surface. While some fibers of the posterior head do appear to have arisen here, most muscle fibers are believed to have originated from the chondrocranium. The pars profunda apparently had a well defined fleshy insertion on a rough, pitted, triangular scar on the medial surface of the coronoid, dorsomedial edge of the prearticular, and possibly pinnately onto the medial surface of the internal tendon (Fig. 7c). The apparent shortness of the re-constructed pars profunda in lateral view is compensated by a pronounced lateral arching over the well developed M. pterygoideus mass and is probably a specialization of the low, wide-skull captorhinids. In addition, it seems likely that the M. pseudotemporalis profunda reached its resting fiber length when the mandible was fully, or almost fully, depressed.

M. intramandibularis

The large teiid lizard *Tupinambis* has a large muscle that is usually identified as the M. intramandibularis. It is not thought to be homologous with the M. intramandibularis of turtles or crocodilians. No other lepidosaurian reptile is known to possess such a muscle. The M. intramandibularis of *Tupinambis* is believed to be a development of the M. adductor mandibulae posterior (Ingeborg Poglayen-Neuwall, 1954; Schumacher, 1973) rather than a part of the M. adductor mandibulae internus. Both turtles and crocodiles have an M. intramandibularis derived from the M. adductor mandibulae internus. In turtles it is a relatively small muscle that lies within the restricted Meckelian canal and adductor fossa in contrast to the form in crocodilians where the M. intramandibularis is much more massive and fills most of the greatly expanded Meckelian canal and adductor fossa. In both groups, the muscle fibers originate from the M. pseudotemporalis lamina of the internal tendon of the basal aponeurosis and insert onto the lateral surface of the Meckelian cartilage.

Eocaptorhinus has a very deep mandible and an adductor fossa that leads anteriorly into a Meckelian canal that is proportionately larger than that of any similar sized modern reptile. Since the Meckelian cartilage, mandibular artery and vein and mandibular ramus of the trigeminal nerve could not be expected to fill more than about 20 percent of the canal, a large M. intramandibularis is proposed to have occupied this volume (Figs. 11 and 14). It would have originated most likely on the insertion tendon of the M. pseudotemporalis superficialis. This tendon may have been sufficiently free to allow it to slide slightly along a smooth channel in the medial surface of the coronoid at the anterior end of the adductor fossa and at the base of the basal aponeurosis. Insertion is presumed to have been on the dorsolateral surface of the Meckelian cartilage.

M. pterygoideus

The M. pterygoideus of modern reptiles is extremely variable in form and has, thus, acquired an equally as varied nomenclature. Table I presents the nomenclatorial system used in this paper, based on Haas' (1973) description of the M. pterygoideus of *Sphenodon*.

In *Sphenodon* there is a large M. pterygoideus typicus and a small M. pterygoideus atypicus (Haas, 1973). Unfortunately, they have often been named the M. pterygoideus anterior and posterior respectively (Adams, 1919; Barghusen, 1973). This has given rise to the expressed opinion that lizards do not possess an anterior component of the M. pterygoideus (Barghusen, 1973) when, in fact, it is the M. pterygoideus

Sphenodon	Lizards	Crocodiles	Cryptodire Turtles	Pleurodire Turtles
M. ptery. atypicus *(M. ptery. ant.)*				
M. ptery. typicus *(M. ptery. post)*	M. ptery. typicus *(M. ptery. post.)*			
M. ptery. sup.	M. ptery. sup.	M. ptery. sup. *(M. ptery. post.)* *(M. ptery. vent.)*	M. ptery. ventr.	
M. ptery. prof.	M. ptery. prof.	M. ptery. prof. *(M. ptery. ant.)* *(M. ptery. dors.)*	M. ptery. dors.	M. ventro-lat. M. rostro-med. M. rostro-lat.

Muscle names in italics have been superceded by more modern terminology.

Table I. Apparent homologies of M. pterygoideus segments in modern reptiles.

atypicus that is missing. This would be of little consequence, in fact only a matter of establishing a synonymy of muscle names, were it not for the fact that Anderson (1936), Ivo Poglayen-Neuwall (1953), Iordansky (1964), and Schumacher (1973a) have used the anterior-posterior terminology for crocodilian pterygoideus musculature without establishing that their partes anterior and posterior were, or were not, the homologues of the similarly named parts of the M. pterygoideus in *Sphenodon* and lizards. As a result, there is no established system of homologies of the parts of the M. pterygoideus as Table I shows. Table I includes a proposed reorganization of the nomenclature of the M. pterygoideus of modern reptiles that establishes the homologies of the segments of these muscles amongst the different groups without the confusion of redefining the partes anterior and posterior. This reorganization is based on a division of the M. pterygoideus into typical and atypical parts in the manner of Ingeborg Poglayen-Neuwall (1953) and Haas (1973). An attempt has been made to include the highly specialized pterygoideus musculature of both cryptodire and pleurodire turtles in this scheme but the veracity of these proposed homologies has not been established with assurance.

The M. pterygoideus atypicus appears to be a unique specialization of *Sphenodon*. There is no evidence to suggest that any fossil reptiles, save perhaps some sphenodontid rhynchocephalians, possessed such a muscle.

Both *Sphenodon* and lizards have a large, often bilaminate, M. pterygoideus typicus. This is the muscle usually referred to as the M. pterygoideus posterior in lizards in allusion to the supposed "loss" of an M. pterygoideus anterior (M. pterygoideus atypicus) that is present in *Sphenodon*, a primitive diapsid reptile, and that was, thus, thought to have been present in all early reptiles. Since it is now considered unlikely that a pars atypicus was present in early reptiles, it is best to regard the large muscle in lizards to be the M. pterygoideus typicus. Since this muscle is considered to be the primitive or typical condition, and the small anterodorsal muscle segment in *Sphenodon* the derived or atypical condition, the M. pterygoideus typicus will, henceforth, be termed simply, the M. pterygoideus.

The M. pterygoideus of *Sphenodon* is a massive muscle that appears to be divided into two units. These divisions are not distinct nor have they been described in detail. Haas (1973) makes it clear that there are two distinct origins that appear to be comparable to those observed in the lizards *Iguana* and *Tupinambis* and described by Lakjer (1926) in *Uromastix*. The muscle fibers originating anterolaterally from the posteroventral surface of the ectopterygoid and the ventromedial surface of the transverse flange of the pterygoid correspond to the fibers of the M. pterygoideus superficialis of *Uromastix* (Lakjer, 1926), *Iguana*, and *Tupinambis*. The fibers of the M. pterygoideus superficialis in lizards and the corresponding muscle segment in *Sphenodon* extend posteroventrolaterally from their origin to form a large masticatory cushion on the ventral surface of the angular where they curve posterodorsally, thence, medially to insert onto the articular and angular ventral to the mandibular articulation. A large superficial tendon ensheathes most of the anteroventral surface of the M. pterygoideus superficialis. It serves as an additional site of origin for the more superficial muscle fibers.

Both *Sphenodon* and lizards have medial fibers of the M. pterygoideus that originate from the ventrolateral surface of the pterygoid, the lateral surface of the quadrate ramus of the pterygoid, and the lateral surface

M. pterygoideus profundus in *Uromastix*, a term that can be used in identifying the muscle fibers in some lizards including *Iguana* and *Tupinambis* and probably also in *Sphenodon*. These muscle fibers extend ventrally to insert onto the medial surface of the angular and, where present, the prearticular. There is little tendon associeated with the predominantly fleshy origin and insertion.

The M. pterygoideus of crocodilians is essentially similar in construction, but much different in size from that of *Sphenodon* and lizards. The origins and insertions are generally the same although a large anterior slip of the pars profunda originates high on the dorsal surface of the pterygoid beneath the eye. Typically the M. pterygoideus has been divided into a pars anterior and a pars posterior (Anderson, 1936; Ivo Poglayen-Neuwall, 1953; Iordansky, 1964) or occasionally a pars dorsalis and a pars ventralis (Lakjer, 1926; Schumacher, 1973) that appear to be the homologues of the M. pterygoideus profundus and M. pterygoideus superficialis respectively, of *Sphenodon* and lizards. It is the lack of correlation between the M. pterygoideus posterior of crocodilians (M. pterygoideus profundus) and the M. pterygoideus posterior of lizards (M. pterygoideus typicus) that Barghusen (1973) found so confusing.

The extensive modification of the M. pterygoideus of turtles, attendant with the extreme re-modelling of the palate has hindered previous attempts at establishing homologies. Table I presents the proposed homologies of the M. pterygoideus of both pleurodire (*Podocnemis*) and cryptodire turtles. Much further research must be pursued before these can be accepted with certainty.

Eocaptorhinus laticeps apparently had an M. pterygoideus typicus similar to that of *Sphenodon* and lizards. It appears to have been sub-divided into a pars profunda and a pars superficialis (Fig. 11). The M. pterygoideus profundus had a fleshy origin on the lightly pitted lateral surface of the ventrolaterally sloped quadrate ramus of the pterygoid, on the ventrolateral edge of the epipterygoid, and on the more heavily pitted dorsal surface of the transverse flange of the pterygoid posterior to the attachment ridge of the orbitotemporal membrane (Fig. 13). The muscle fibers are believed to have extended ventromedially and slightly posteriorly to insert onto the medial surface of the internal tendon posterior to the M. pseudotemporalis profundus insertion and fleshily onto the anterodorsal surface of the articular at the base of the angular process and onto the medial surface of the prearticular. At no time did the M. pterygoideus extend anteriorly below the orbit as it does in crocodilians and cryptodire turtles (Schumacher, 1973a) or as it apparently did in labyrinthodont amphibians (Panchen, 1970).

The M. pterygoideus superficialis was a large muscle that apparently originated tendinously from the medial and ventral edges of the transverse flange and quadrate ramus of the pterygoid (Figs. 13, 15, and 16). Some medial fibers seem to have had a narrow fleshy insertion on the slightly pitted ventral surface of the neck of the pterygoid. Laterally, the pars superficialis probably was sheathed by a long narrow tendon that extended posterior to lie in a marked groove in the ventral surface of the prearticular immediately medial to its sutural contact with the angular. The tendon inserted onto the ventral surface of the retroarticular process of the articular just as in modern lizards. The muscle fibers of the pars superficialis extended posteroventrolaterally toward their insertion.

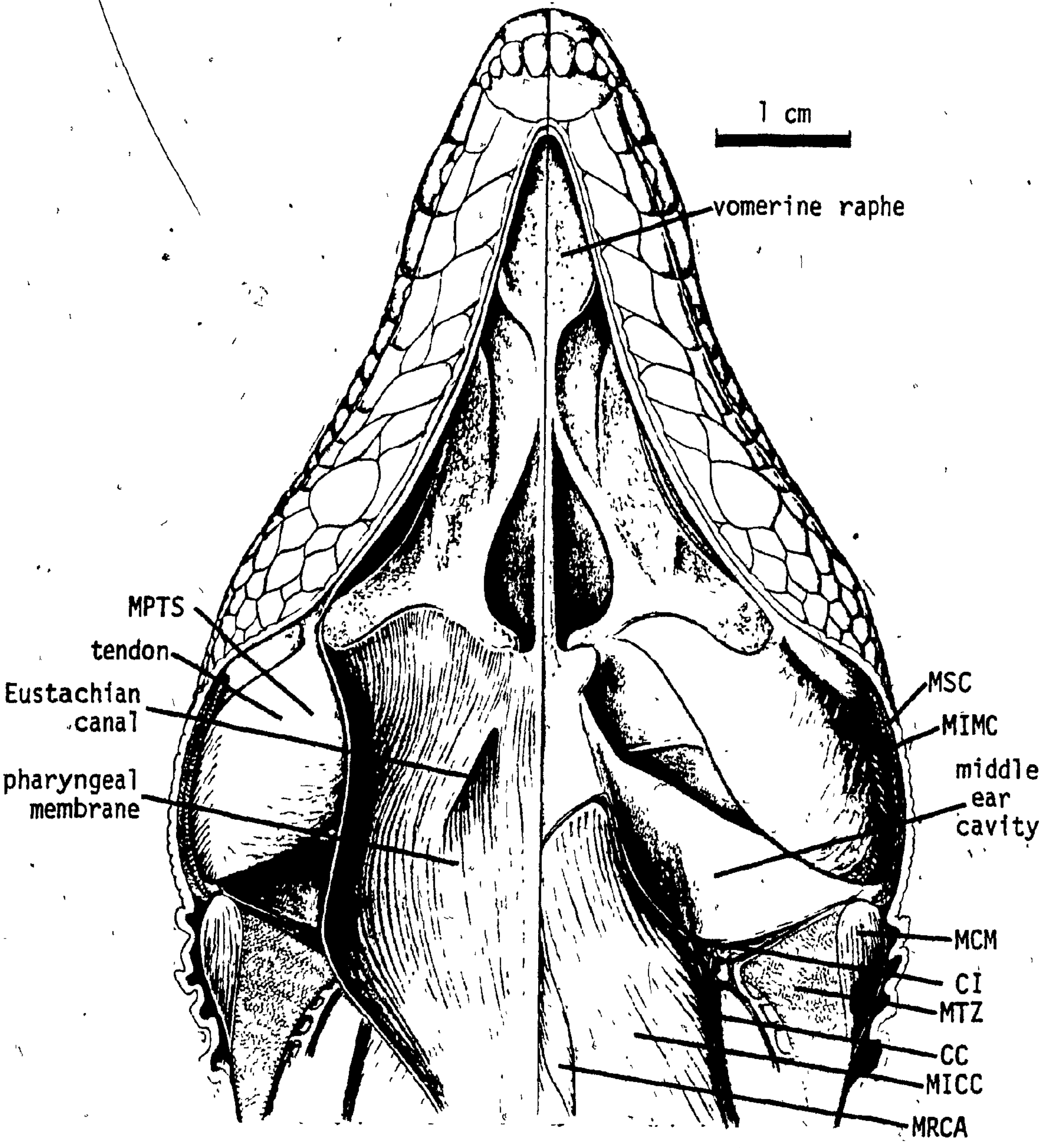


Figure 15. *Eocaptorhinus laticeps*. Head in ventral aspect showing M. pterygoideus. Reconstruction.

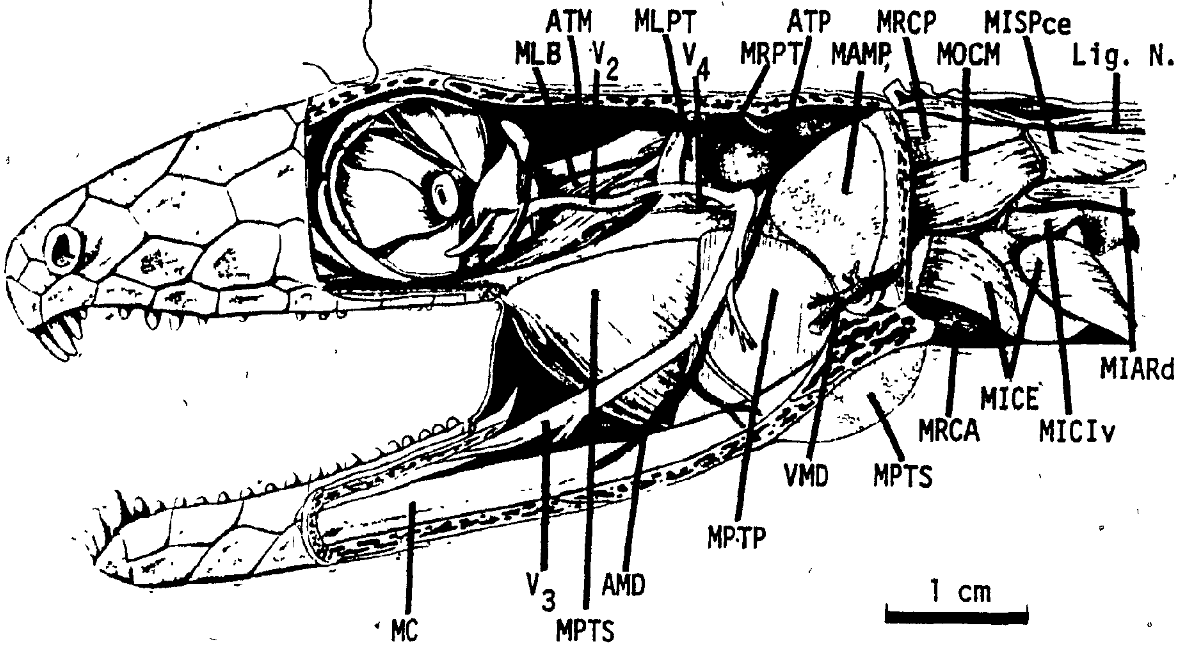


Figure 16. *Eocaptorhinus laticeps*. Head in lateral aspect showing the M. pterygoideus divisions and constrictor dorsalis musculature. Reconstruction.

Deep fibers would have formed a thick ventral masticatory cushion that had a fleshy insertion onto the heavily scarred prearticular portion of the ventral surface of the angular process. More shallow fibers apparently arched ventrally over the large mass of the deep fibers to form a deep recumbent fold against the lateral surface of the angular at which point they inserted onto the ventral surface of the most posterior part of the angular and onto the long tendon (Fig. 11). The whole of the masticatory cushion is thought to have been covered by a broad tendon, just as in modern reptiles, that attached to the posterior rim of the articular portion of the angular process and to a prominent longitudinal ridge on the angular that separated the sculptured, skin-covered surface from the rough insertional region of the shallow fibers of the pars superficialis (Fig. 15 and 16).

The M. pterygoideus superficialis is believed to have reached its maximum resting fiber length when the mandible was fully depressed. The strongly curved muscle fibers, even though heavily tendon supported superficially, were of sufficient length to have allowed such elongation. Since this muscle was not the only mandibular adductor, it could be passively compressed by the M. pseudotemporalis and M. adductor mandibulae externus after reaching its minimum active contracted length.

M. constrictor dorsalis

The M. constrictor internus dorsalis or as it is more commonly and simply known, the M. constrictor dorsalis, is not strictly part of the mandibular adductor complex. Rather than being innervated by the mandibular ramus (V_3) of the trigeminal nerve, the M. constrictor dorsalis group is innervated by its own, unnumbered (except by Lakjer, 1926, who called it the V_4) ramus of the trigeminal nerve. Typically it consists of three distinct parts, the M. levator bulbi, M. levator pterygoidei, and M. protractor pterygoidei. They lie medial to the maxillary ramus (V_2) of the trigeminal nerve and lateral to the ophthalmic ramus (V_1), not medial to the ophthalmic ramus as Säve-Söderbergh (1945; Gomes, 1972; Haas, 1973) has indicated. These muscles are intimately associated with cranial metakinesis in *Sphenodon* (Versluys, 1912; Ostrom, 1962) and lizards (Lakjer, 1926; Frazzetta, 1962). In modern reptiles where metakinesis has been lost during ontogeny as in *Sphenodon* (Versluys, 1912b; Ostrom, 1962) or during phylogeny as in turtles and crocodiles (Schumacher, 1973a) the members of the M. constrictor dorsalis group may be partially or completely lost. In *Sphenodon* old akinetic individuals may have an atrophied M. protractor pterygoidei or even may have lost it entirely (Versluys, 1912b; Ostrom, 1962). The other muscles are seemingly unaffected. In turtles, some remnants of the M. constrictor dorsalis group may be seen only in the embryonic stages (Fuchs, 1915; Edgeworth, 1935; Schumacher, 1973a). In contrast, crocodilians retain a post-embryonic segment of the M. levator bulbi, although the M. protractor pterygoidei and M. levator pterygoidei, which are normally associated with metakinesis have been lost.

While there is evidence that *Eocaptorhinus* possessed both an M. levator pterygoidei and an M. protractor pterygoidei, there is no such evidence either to confirm or deny the presence of an M. levator bulbi. Since an M. levator bulbi is present in all modern reptiles in which one or more of the other components of the M. constrictor dorsalis group are retained, albeit often with considerable reorganization, an M. levator bulbi is believed also to have been present in *Eocaptorhinus*. The M. levator bulbi of modern reptiles typically originates from a tendon and inserts onto the ventral surface of the bulb of the eye. It thus generally leaves no evidence of its presence, and for this reason, is not included in this description.

M. levator pterygoidei

In *Sphenodon* and lizards, the M. levator pterygoidei originates from the lateral surface of the chondrocranium medial to the dorsal tip of the columella of the epipterygoid. Only in akinetic lizards which lack an epipterygoid such as the Chamaeleonidae, is the M. levator pterygoidei absent (Ingeborg Poglayen-Neuwall, 1954; Haas, 1973). It has a fleshy insertion on the medial surface of the base of the epipterygoid and, in lizards, marginally onto the dorsal edge of the quadrate ramus of the pterygoid slightly anterior and posterior to the epipterygoid-pterygoid articulation.

In *Eocaptorhinus* the epipterygoid was massively built and well sutured to, rather than loosely articulated with, the pterygoid. The M. levator pterygoidei apparently originated from the lateral surface of the chondrocranium medial to the dorsal tip of the columella of the epipterygoid just as in modern lizards and *Sphenodon*. A large parabolic depression marked by many well developed Sharpey's fiber pits on the lateral surface of the wide triangular base of the epipterygoid is believed to have been the insertion scar of a rather large M. levator pterygoidei (Figs. 11 and 13).

M. protractor pterygoidei

The M. protractor pterygoidei of *Sphenodon* and lizards typically originates from the crista alaris of the prootic and inserts on the dorsal edge of the quadrate ramus of the pterygoid immediately anterior to the quadrate (Lakjer, 1926; Oelrich, 1956; Ostrom, 1962; Haas, 1973).

Its muscle fibers are extremely short in metakinetic forms but may be atrophied and greatly reduced or even lost if kinesis is lost during the lifetime of the animal (Ostrom, 1962; Haas, 1973). An M. protractor pterygoidei does not develop in turtles and crocodilians (Lakjer, 1926; Haas, 1973).

The crista alaris of the prootic and the anterior edge of the prootic portion of the paroccipital process are well developed in *Eocaptorhinus*. They lie just dorsomedial to the dorsal edge of the quadrate ramus of the pterygoid. These regions are not known in great detail in *Eocaptorhinus* so that muscle origin and insertion scars have not been seen. It is believed that cranial metakinesis was present but was relatively poorly developed in juveniles and was lost in adults as the median ascending process of the supraoccipital, the paroccipital processes, and the stapes ossified. The M. protractor pterygoidei, if present at all, was probably poorly developed, at least in adult animals.

Discussion

The reconstruction of musculature in fossil vertebrates is always a difficult task fraught with the dangers of over extension of available information and circular reasoning. Nevertheless, an attempt must be made to increase our knowledge of the biology of these animals, in the context of their living, functioning existence, through the study of fine anatomical detail, even in the face of these possible shortcomings. In a discipline more attuned to the description of suture patterns and general outlines of bones and to the recognition of new taxa and the development of broad phylogenetic schemes, the biologic aspects of the study of fossil reptiles are, unfortunately, too often forgotten.

Attention to the fine detail of preserved remains reveals far more biological information than has generally been appreciated. Careful cross referencing of anatomical characters of the fossils with the observed structure of modern reptiles permits accurate re-construction of soft structures when all functional and spacial limitations are satisfied.

That the mandibular adductor system of *Eocaptorhinus laticeps* more closely resembles that of the sphenodontid rhynchocephalian *Sphenodon* and, to a slightly lesser extent, unspecialized lizards, is not surprising in view of the similarities in size and generally insectivorous feeding mode. Numerous differences do occur, especially as related to the development of temporal fenestrations in the modern forms. The drastic re-arrangement of the braincase of modern crocodilians and the specialized aquatic feeding pattern have altered the adductor musculature so greatly that only general similarities can be recognized. Although turtles are nominally regarded as "anapsids", their feeding mechanisms and cranial osteology are so specialized, with respect to the primitive captorhinomorph pattern that, as in crocodilians, little other than the most general characteristics of the adductor musculature can be compared.

Perhaps the most significant observation that can be made about the mandibular adductor system of *Eocaptorhinus laticeps* and other early captorhinomorph reptiles is that it was at least equally as complex and sub-divided as is the adductor musculature of any modern reptile. For the first time, a primitive reptile has been found in which muscle attachment scars can be identified with confidence. There is no evidence that the primitive mandibular adductor was an arrangement of three unidirectional, undifferentiated muscles as has so often, of necessity been assumed in the absence of detailed information (Adams, 1919; Olson, 1961; Carroll, 1969; Barghusen, 1972). If anything, a tendency toward simplification of mechanical systems and related adductor musculature appears to be observable, particularly amongst turtles and, apparently, mammal-like reptiles.

The M. adductor mandibulae of *Eocaptorhinus laticeps* was, for the most part, typical of primitive non-synapsid reptiles. The large M. adductor mandibulae externus apparently was divided into three main parts. The pars superficialis originated from the lateral margin of the parietal. The bipartite pars media had a lateral origin on the parietal and a medial origin on the anterior face of the supraoccipital. The temporal artery separated sub-divisions A and B of the pars media. The pars profunda inserted onto the lateral surface of the supraoccipital and the anterodorsal surface of the paroccipital process.

Although the cranial musculature of synapsid reptiles has not been described in detail, some observations have been made on the development of various muscle segments. In contrast to the form of the M. adductor mandibulae externus of non-synapsid reptiles, that of primitive synapsids (pelycosaurs) appears to have consisted of a single unit, the origin, on the lateral edge of the ventral surface of the parietal, and the insertion of which, on the lateral surface of the external tendon and mandible, would seem to identify it as the spacial equivalent, and thus in Lakjer's (1926) sense the homologue, of the M. adductor mandibulae externus superficialis of non-synapsid reptiles. There is no evidence that either a pars media or a pars profunda existed in synapsids. These differences in the M. adductor mandibulae externus appear to be closely related to the profound differences in the structure and mechanics of the braincases of primitive non-synapsid and synapsid reptiles. In non-synapsid reptiles where the large M. adductor mandibulae externus medius and profundus originate from the supraoccipital and the paroccipital process, the occiput is typically vertical with a narrow supraoccipital that contacts only the postparietals. The paroccipital processes are slender and the post-temporal fenestrae, consequently, very large. In synapsid reptiles, the M. adductor mandibulae externus medius and profundus apparently were not developed. The occiput sloped anterodorsally into the region that would have been occupied by the partes media and profunda in non-synapsid reptiles. In the absence of these muscle segments, the supraoccipital and the paroccipital processes expanded to close most of the post-temporal fenestra and produce the typically synapsid plate-like occiput with the supraoccipital typically becoming sutured to the postparietals (interparietal) and tabulars and the paroccipital process to the tabulars and quadrate (Romer and Price, 1940).

The M. pseudotemporalis of *Eocaptorhinus* apparently was sub-divided into a large dorsal pars superficialis and a smaller, ventromedial pars profunda. The pars superficialis, thus, was a prominent muscle in both non-synapsids and synapsids in contrast to the pattern proposed by Barghusen (1972). Rather than developing after the formation of the dorsal temporal fenestra in diapsids, it appears to have been a large muscle that was an important factor in the rapid enlargement and later investment of the fenestra. In non-synapsid reptiles, the M. pseudotemporalis superficialis became the major muscle in the anterior half of the adductor chamber while the M. adductor mandibulae externus medius and profundus became the major posterior muscles, all of which lay medial to a relatively thin pars superficialis. In synapsid reptiles, the medial half of the adductor chamber apparently was filled by the M. pseudotemporalis superficialis and the lateral half by the M. adductor mandibulae externus superficialis. A small M. adductor mandibulae posterior occupied the posteroventral portion of the adductor chamber in both synapsid and non-synapsid reptiles.

The braincases of primitive reptiles (Heaton, 1975, 1978) formed a loose metakinetic articulation with the skull roof as Versluys (1912a, b) had expected, based on his study of modern reptiles. The absence of a long, restricting median ascending process of the supraoccipital and the presence of poorly ossified, laterally projecting paroccipital processes permitted the braincase to rotate relative to the skull in small captorhinomorphs. As captorhinomorphs grew larger during their evolutionary history, particularly amongst the Captorhinidae, a large median ascending process was developed and the paroccipital processes became fully ossified, thus, eventually preventing any form of metakinesis. *Eocaptorhinus* represents an intermediate stage in this sequence in which a moderately large median ascending process of the supraoccipital and fully ossified paroccipital processes probably restricted or even prevented metakinesis in adult animals. Juveniles are believed to have had metakinetic skulls as had the primitive captorhinid *Romeria*, from the holotype specimen of which the loosely articulated braincase was lost during preservation (Clark and Carroll, 1973). Primitive captorhinomorphs such as *Paleothyris* (Carroll, 1969) and *Protorothyris* (Clark and Carroll, 1973) likewise appear to have had metakinetic skulls. *Sphenodon* and many lizards have developed the paroccipital processes as the metakinetic axis, something that could not be accomplished by captorhomorphs in which the paroccipital processes were not fully ossified. Captorhinomorphs appear to have had a more dorsal metakinetic axis along the dorsal edge of the supraoccipital where it contacted the postparietal. In all metakinetic reptiles excessive movement between the skull roof and the braincase must be prevented. Limitation of this movement has been accomplished in *Sphenodon* and most lizards by the development of accessory structures on the dorsolateral edge of the crista alaris of the supraoccipital that contact the medial, descending flange of the parietal when the skull roof is fully elevated. This is possible with the low metakinetic axis of modern lepidosaurs but was not applicable to captorhinomorph metakinesis. Instead, extensive relative posterior movement of the ventral portion of the braincase at maximum skull roof elevation was accomplished by use of the massively ossified posteroventrolaterally directed stapes. The use of the stapes as a mechanical link in a kinetic skull is a primitive character exhibited by rhipidistian fish. The use of the stapes as a stabilizing unit is believed to have reached its maximum in the gigantic late Permian captorhinid *Labidosaurikos meachami* (Stovall, 1950) in which the stapes is suturally attached to the basisphenoid, prootic, opisthotic (paroccipital process), and apparently the quadrate. Such metakinesis is a functional necessity amongst small, insectivorous, terrestrial tetrapods that employ inertial feeding since it allows the caniniform teeth to be accelerated down upon the prey item at the same time the mandible is being raised (Frazzetta, 1962). Modern lizards represent the culmination of such a metakinetic mechanical system with the introduction of an additional mesokinetic articulation between the frontal and parietal. The muscle fibers of the M. adductor mandibulae externus medius and profundus and the M. adductor mandibulae posterior all originate from the braincase in the earliest reptiles. It is, therefore, necessary to know with the greatest possible confidence, the configuration of these muscles if the mechanics of the braincase and its metakinesis are to be understood. Turtles apparently have followed a course of braincase immobilization at an anapsid grade of development similar to that of captorhinids as did pareiasaurs. Although both groups appear to have separated early from the same basic non-synapsid stock, they share many common features indicative of a primitive metakinetic heritage. In particular, they possess high narrow supraoccipitals and large post-temporal fenestrae that are correlated with the possession of metakinesis and well developed partes media and profunda of the M. adductor mandibulae externus in *Sphenodon*, lizards, captorhinomorphs, and perhaps even primitive procolophonids (Ivakhnenko, 1972). Large size appears to be the primary factor controlling the degree of metakinetic movement, apparently because of the limitations in the size and strength of the constrictor dorsalis musculature which is the major skull roof elevator. Closely associated with size increase is the development of herbivorous and carnivorous feeding modes, the former requiring great adduction power but not metakinesis, the latter often placing extreme loads on the skull roof and braincase. In both cases, metakinesis is of little practical advantage and may, on occasion be a distinct disadvantage. It is, therefore, not surprising that few reptiles with skull lengths of over about 10 cm retained metakinetic skulls. The exceptions include platynotan lizards (varanids and mosasaurs), the former with extremely light weight truss structure skulls, the latter aquatic forms where natural bouyancy reduced the significance of increased size and weight. The only other known exceptions are the saurischian dinosaurs in which the metakinetic system was modified considerably and a mesokinetic (fronto-parietal) joint also developed. This arrangement is retained in modern birds.

Functionally, the trigeminally innervated muscles of modern non-synapsid reptiles and apparently also *Eocaptorhinus,* appear to be divisible into four major groups: (1) skull roof elevators; (2) mandibular accelerators; (3) mandibular power adductors; and (4) mandibular stabilizers. The skull roof elevators are the posterior members of the M. constrictor dorsalis group, the M. levator pterygoidei and, if present in *Eocaptorhinus,* the M. protractor pterygoidei. Two muscles function as mandibular accelerators during the adduction cycle, the M. pterygoideus, a massive muscle that initiates the movement, and the much thinner M. adductor mandibulae externus superficialis that maintains the adduction speed initially imparted to the mandible by the M. pterygoideus. Power for crushing or shearing resistant food items is provided by the massive M. pseudotemporalis, and more posteriorly attached M. adductor mandibulae externus medius and profundus. Particularly resistant food items or struggling prey may provide forces that might potentially strain or even disarticulate the articular-quadrate joint. The M. adductor mandibulae posterior serves as a major mandibular stabilizer holding the joint in position during jaw adduction.

Conclusions

Eocaptorhinus laticeps is a captorhinomorph reptile of the family Captorhinidae known from numerous superbly preserved specimens from the lower Permian deposits of northcentral Texas and central Oklahoma. The immense amount of fine detail available from these specimens has permitted reconstruction of the adductor mandibulae musculature with a high degree of confidence. As in all modern reptiles, it was a complex muscle mass divided into three major units, the M. adductor mandibulae posterior, M. adductor mandibulae externus, and M. adductor mandibulae internus. The M. adductor mandibulae posterior was a simple undifferentiated muscle. The M. adductor mandibulae externus apparently was of tripartite form with partes superficialis, media, and profunda, the latter two parts originating, at least in part, from the braincase and bulging into the large post-temporal fenestrae. The M. adductor mandibulae internus was divided into two distinct units, the M. pseudotemporalis and the M. pterygoideus, both of which were bipartite in form. The M. pseudotemporalis superficialis was a large muscle that originated from the lateral surface of the anterior braincase and bulged laterally up against the ventral surface of the parietals but was not attached to them. The pars profunda was a small ventromedial segment. The M. pterygoideus had both superficial and deep parts that expanded ventrolaterally about their insertion to form a prominent masticatory cushion. In addition, prominent constrictor dorsalis musculature connected the palate-skull roof complex to the braincase.

These muscular characteristics are intimately related to the osteological characters that differentiate this non-synapsid reptile from a primitive synapsid reptile. The occipital surface is nearly vertical. The supraoccipital, on which much of the M. adductor mandibulae externus medius and profundus originates, is narrow with consequently large post-temporal fenestrae. In contrast, primitive synapsid reptiles have steeply sloped, anterodorsally arched, plate-like occiputs with wide supraoccipitals and consequently tiny post-temporal fenestrae. This is apparently, the result of the absence of the M. adductor mandibulae externus medius and profundus in the synapsid lineage.

Metakinesis was a major functional characteristic of primitive reptiles that was further developed by some non-synapsid lineages. The family Captorhinidae was an early specialization of the basic non-synapsid radiation in which the metakinesis was progressively lost as increasingly larger members of the family appeared. Other non-synapsid reptiles including pareiasaurs, turtles, and crocodilians also followed a similar history of braincase immobilization and M. constrictor dorsalis reduction as they evolved out of the small, terrestrial, insectivore niche to which they were primitively adapted. The earliest synapsids that are adequately known had already adapted to a carnivorous feeding mode. These apparently were accompanied by herbivorous types that had also solidified the primitive metakinetic braincase-skull roof junction by expanding the supraoccipitals and paroccipital processes and suturing them to the large tabular. In the synapsid lineages, the M. constrictor dorsalis probably was lost with the early attainment of an akinetic skull.

The non-synapsid and synapsid reptiles may be separated at least as far back as the earliest appearance of reptiles in the fossil record. The osteological characteristics of the skulls of these groups are determined to a large degree by the configuration of the adductor mandibulae musculature.

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CRANIAL KINESIS
IN
PRIMITIVE REPTILES

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Abstract

Cranial metakinesis, movement between the skull roof (maxillary segment) and braincase (occipital segment) of the skull, was a primitive reptilian characteristic. It developed in association with small size which was a prerequisite for the development of the amniotic egg. There was a selective advantage to adapting the loose braincase-skull roof junction of tiny reptilian ancestors to a refined gape orienting mechanism that permitted near simultaneous tooth impact onto prey and little energy loss in unnecessary acceleration of prey items during capture. Excessive skull roof elevation was prevented by the positioning of the dorsoventrolaterally directed stapes preventing it from functioning as an auditory ossicle as it did im many later groups of reptiles.

Multisegmented mandibular adductor musculature was required to permit efficient metakinesis. A vertical occiput with large post-temporal fenestrae reflected the presence of a large M. adductor mandibulae externus medius and profundus. Large size limited the ability of the constrictor dorsalis musculature to elevate the skull roof leading to akinesis while retaining the primitive reptilian occipital pattern. Akinesis developed in small primitive synapsids in respose to heavy stresses encountered as a result of their active, carnivorous feeding mode. The plate-like occiput of pelycosaurs was sloped anterodorsally. The post-temporal fenestrae were small in response to the loss of the partes media and profunda of the M. adductor mandibulae externus.

The structure of the occiput and the evidence it bears on the history of metakinesis in the evolution of any group of primitive tetrapods allows a renewed assessment of the phylogenetic position of many groups. It appears that diadectids, tseajaiids, limnoscelids, and seymouriamorphs form a single coherent group of amphibians, the true cotylosaurs. Procolophonids and pareiasaurs are true but extremely primitive reptiles and are not cotylosaurs.

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CRANIAL KINESIS IN PRIMITIVE REPTILES

INTRODUCTION

The study of cranial kinesis in modern reptiles, which was begun by Versluys (1912a, b, 1927), has been pursued in depth only recently. Frazzetta's study (1962) of the kinetics of the skull of modern lizards, and in particular the extremely mobile form *Varanus indicus*, is the most detailed to date. Both Versluys and Frazzetta recognized two major types of kinesis in lizards: metakinesis, movement between the braincase and posterior skull roof (parietals) and mesokinesis, movement between the frontals and the parietals. Additional types of kinesis are present in some groups of lizards and snakes. Only meta- and mesokinesis are common to most groups of lizards; neither is present in snakes. Modern turtles and crocodilians are akinetic. Except for Versluys (1910, 1912a, b, 1927, 1936) investigation of the possible mesokinesis in carnosaur dinosaurs, little has been mentioned of the cranial kinesis in fossil reptiles. Gow recognized the existence of metakinesis in milleretids (1972) and in younginid and prolacertid eosuchians (1975). Ivakhnenko (1973) noted definite metakinesis in *Tichvinskia vjatkensis*, an early member of the primitive reptilian family Procolophonidae. His claims of a mesokinetic fronto-parietal union are, however, hard to substantiate from a structural point of view. Amongst members of the primitive reptilian sub-order Captorhinomorpha, cranial kinesis was well developed in small, primitive forms although it has been mentioned only as "probably possible" by Carroll (1969c).

Primitive captorhinomorph reptiles are thought to have been the ancestors of modern crocodiles, lizards, rhynchocephalians, and snakes (Carroll, 1969a, b, c; Reisz, 1977). Whether modern turtles have evolved from captorhinomorph ancestors has not been established. At least part of the reason for the enormous success of reptilian lineages developed from a primitive captorhinomorph stock is the presence, unless secondarily reduced (e.g. crocodilians) of well developed cranial kinesis within this group. If the great radiation of captorhinomorph descendants, including dinosaurs, birds, pterosaurs, nothosaurs, and plesiosaurs among other fossil groups as well as modern reptiles (except turtles), is to be understood, an insight into the basic mechanism that gave this group its great competitive advantage over contemporary forms must be gained.

Hylonomus lyelli and *Paleothyris acadianum* from the early to middle Pennsylvanian of Nova Scotia are the most primitive members of the captorhinomorph lineage (Carroll, 1964, 1969a, b; Carroll and Baird, 1972). The known specimens of these animals are all disarticulated and fragmentary although individual bones are usually well preserved. By using these bones and information on the structure of the captorhinomorph braincase obtained from a study of superbly preserved specimens of the advanced captorhinomorphs *Eocaptorhinus laticeps* (Heaton, 1975, 1978) and *Captorhinus aguti* (Price, 1935) of the family Captorhinidae from the middle lower Permian deposits of Texas and Oklahoma, it is possible to reconstruct a braincase and skull roof, with a high degree of confidence, that would have been typical of many and perhaps all primitive captorhinomorphs. Such a braincase and skull roof would not be significantly different from that of the primitive captorhinid reptile *Romeria prima* (Clark and Carroll, 1973). *Eocaptorhinus laticeps*, although its osteological and myological structure is much better known that that of the more primitive forms, is not used here as the model of primitive captorhinomorph cranial structure since, in correlation with its relatively large size, the primitive cranial metakinesis had been greatly reduced and probably even lost in the adult. Much as the adult *Sphenodon*, a modern sphenodontid rhynchocephalian, is akinetic while the juvenile is metakinetic (Versluys, 1912b; Ostrom, 1962), so too is it thought that the juvenile *Eocaptorhinus* was metakinetic. Certainly the smaller ancestors of *Eocaptorhinus*, *Romeria prima*, *R. texana*, and *Protocaptorhinus (= Puercosaurus?) pricei* were metakinetic even as adults. Differences in muscle architecture between *Eocaptorhinus* and a *Hylonomus*-like generalized, primitive captorhinomorph are believed to have been minimal. Such differences as do appear to have existed are discussed.

SKULL AND CRANIAL MUSCULATURE OF CAPTORHINOMORPHS

The skulls of numerous primitive captorhinomorphs including *Hylonomus* (Carroll, 1964), *Paleothyris* (1969a, b, 1970), *Brouffia*, *Cephalerpeton*, *Anthracodromeus*, *Coelostegus* (Carroll and Baird, 1972) and *Protorothyris* (Clark and Carroll, 1973) are known; several in considerable detail. Braincase material is present in *Hylonomus*, *Paleothyris*, *Coelostegus*, and *Protorothyris* as well as in an undescribed *Hylonomus*-like, primitive captorhinomorph from the Pennsylvanian of Colorado (Vaughn, personal communication). Well preserved skull and braincase material of the more advanced captorhinomorph *Eocaptorhinus* has been described by Heaton (1975, 1978).

As in the modern sphenodontid rhynchocephalian *Sphenodon punctatus*, the skulls of captorhinomorphs, both primitive and advanced, were composed of three functional units (Fig. 1). The "occipital segment" consisted of the braincase made up of the supraoccipital, exoccipitals, opisthotics, basioccipital, prootics, parasphenoid, and basisphenoid but not the anterior braincase (Fig. 2). The "maxillary segment" was composed of the remaining

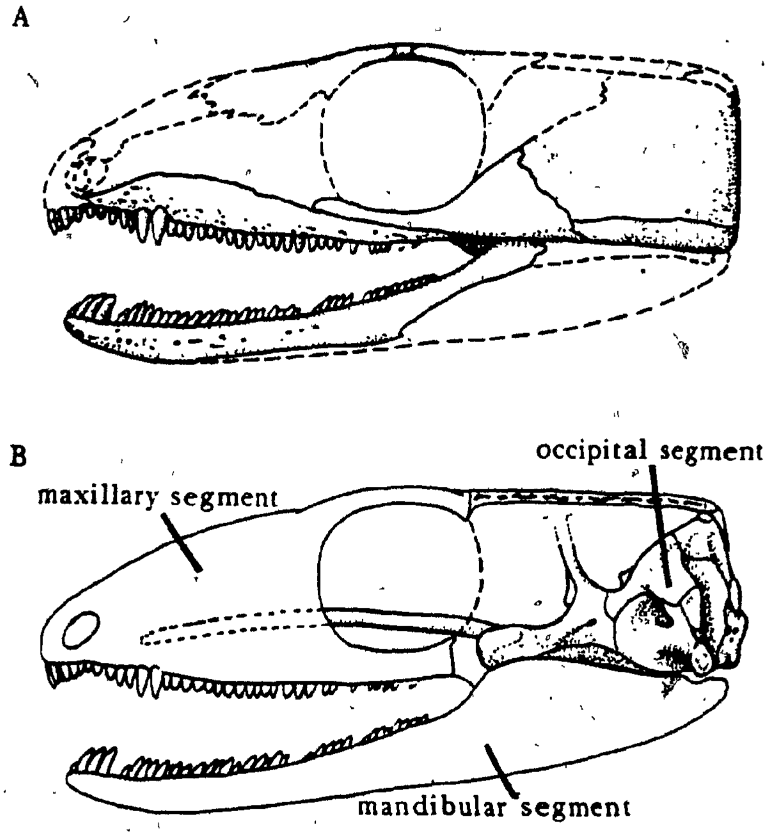


Figure 1. Skull in lateral aspect of the primitive captorhinomorph reptile *Hylonomus lyelli*. a) Reconstruction. b) Functional units.

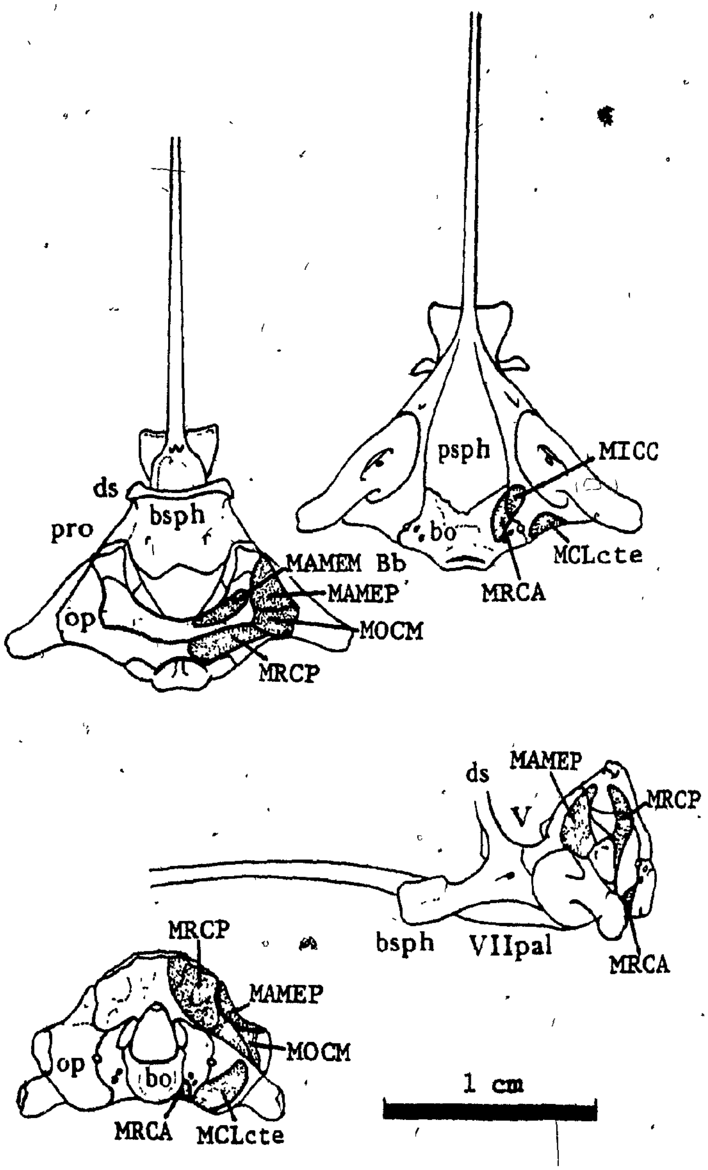


Figure 2. Primitive captorhinomorph reptile braincase with muscle origins indicated. Composite reconstruction.

bones of the skull. The "mandibular segment" was formed solely from the mandible. There appear to have been few significant differences amongst the braincases of the primitive captorhinomorphs. In general, the opisthotics were not fully ossified but extended cartilaginous paroccipital processes laterally to meet the quadrate. In advanced captorhinid captorhinomorphs, there was an increasing tendency toward ossification of the paroccipital processes correlated with increasing size and decreasing cranial kinesis. A similar association of the development of a prominent medial ascending process of the supraoccipital in captorhinids--this process was absent in primitive captorhinomorphs--with an akinetic skull has also been observed.

Captorhinomorph reptiles, both primitive and advanced, appear to have had a tripartite adductor mandibulae muscle mass (Fig. 3) as do all modern reptiles, including turtles, which may not be captorhinomorph derivatives, and many amphibians. The M. adductor mandibulae was divided into an M. adductor mandibulae posterior, and M. adductor mandibulae externus and an M. adductor mandibulae internus. Both the partes externa and interna were themsleves further subdivided (Fig. 4). All inserted onto the mandible or onto tendons attached ot it. The origins were on either the occipital segment or the maxillary segment. The occipital segment served as the origin for the large M. adductor mandibulae externus medius Ba and the almost equally large M. adductor mandibulae externus profundus. The maxillary segment had four regions of origin. The anterior region of the braincase, in the absence of a medial descending flange of the parietal, as is present in most modern reptiles (gekkonid lizards are an exception), served as the site of origin of the M. pseudotemporalis superficialis.

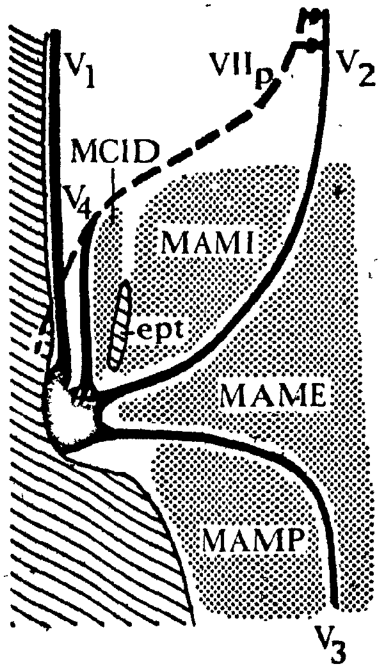


Figure 3. Schematic diagram showing M. adductor mandibulae divisions in frontal section.

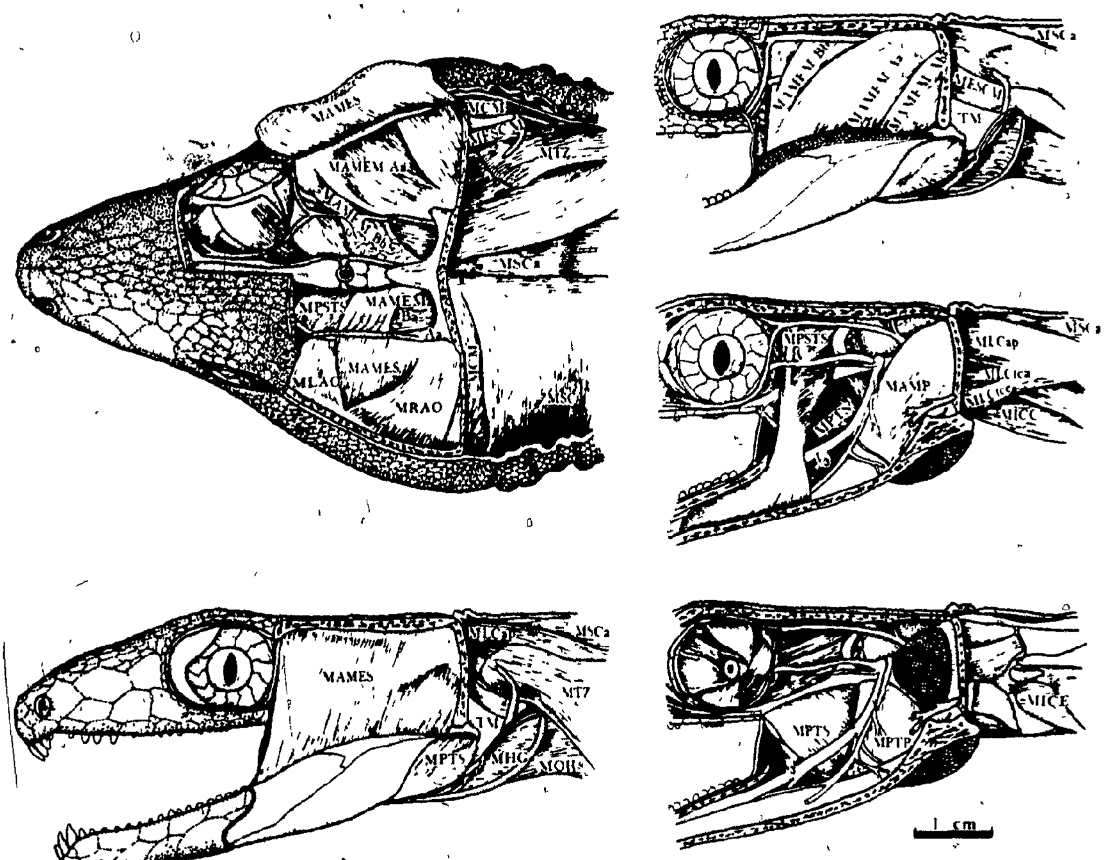


Figure 4. *Eocaptorhinus laticeps*. Skull with reconstruction of M. adductor mandibulae. a) Dorsal aspect. b) Lateral aspect, superficial. c) Lateral aspect, second depth. d) Lateral aspect, third depth. e) Lateral aspect, deep.

The M. adductor mandibulae externus medius Aa, Bb, and the M. adductor mandibulae externus superficialis originated from the skull roof and the M. adductor mandibulae posterior and possibly an M. adductor mandibulae externus medius Ab from the quadrate. The pterygoid functioned as the site of origin of the M. pterygoideus. Two posterior segments of the M. constrictor dorsalis, the M. protractor pterygoidei and M. levator pterygoidei connected the occipital segment (lateral braincase) and the maxillary segment (pterygoid).

Considerable cervical musculature inserted onto the occipital surface of both the occipital and maxillary segments. Dorsally, the M. spinalis capitis, M. latissimus capitis dorsalis, and M. episternocleidomastoideus inserted onto the parietals, post-parietals, and tabulars (where present), all part of the maxillary segment. The M. rectus capitis posterior inserted dorsally onto the supraoccipital, exoccipital, and opisthotic and the M. rectus capitis anterior and M. iliocostalis capitis inserted ventrally onto the basioccipital and exoccipital, all components of the occipital segment. These were the principal muscles that governed braincase movement in the vertical (sagittal) plane. Other cervical musculature controlled movement in the horizontal (frontal) plane including the M. obliquus capitis magnus and M. latissimus capitis transversalis capitis that inserted on the opisthotic and the M. latissimus capitis transversalis cervicus that inserted onto the basioccipital. Rotation of the head in the transverse plane at the occipital condyle is believed to have been limited, as with many modern reptiles. With the possible exception of the M. episternocleidomastoideus, there were no muscles inserting on either the skull roof or the braincase that could have applied significant torsional forces. The cervical musculature was important during feeding as a braincase stabilizing mechanism. In the following discussion of metakinesis, the role of the cervical musculature is not discussed since the braincase is regarded as having been maintained in a fixed position. The cervical muscles would, thus, be activated irregularly to hold the fixed position of the braincase.

The M. cervicomandibularis or its smaller anterior segment the M. depressor mandibulae originated from the fascia overlying the cervical musculature and from the posterior edge of the supratemporal and possibly the parietal. It inserted onto the posterior surface of the articular and, in the case of *Eocaptorhinus* where a prominent retroarticular process was present, the dorsal surface of that process.

The final group of muscles that had a bearing on the cranial mechanics of the primitive captorhinomorph reptile skull were a number of hyoid muscles, in particular the more posteriorly located M. coracohyoideus, M. geniohyoideus, M. omohyoideus, and M. sternohyoideus.

Each group of muscles had a specific major role and often one or more minor roles to play at each point in the adduction-depression cycle. In 1961 Olson introduced the terms "kinetic-inertial" and "static-pressure" to describe two fundamentally different patterns of mandibular adductor muscle structure and dynamics in tetrapods (Fig. 5a). Since a mandibular adductor muscle exerts its greatest force tangentially to the arc of rotation of the mandible about its mandibuloquadrate articulation, the further the origin of the muscle from the articulation relative to the insertion, the greater the angle of mandibular depression possible while maintaining a right angle between the muscle action line and the mandibular

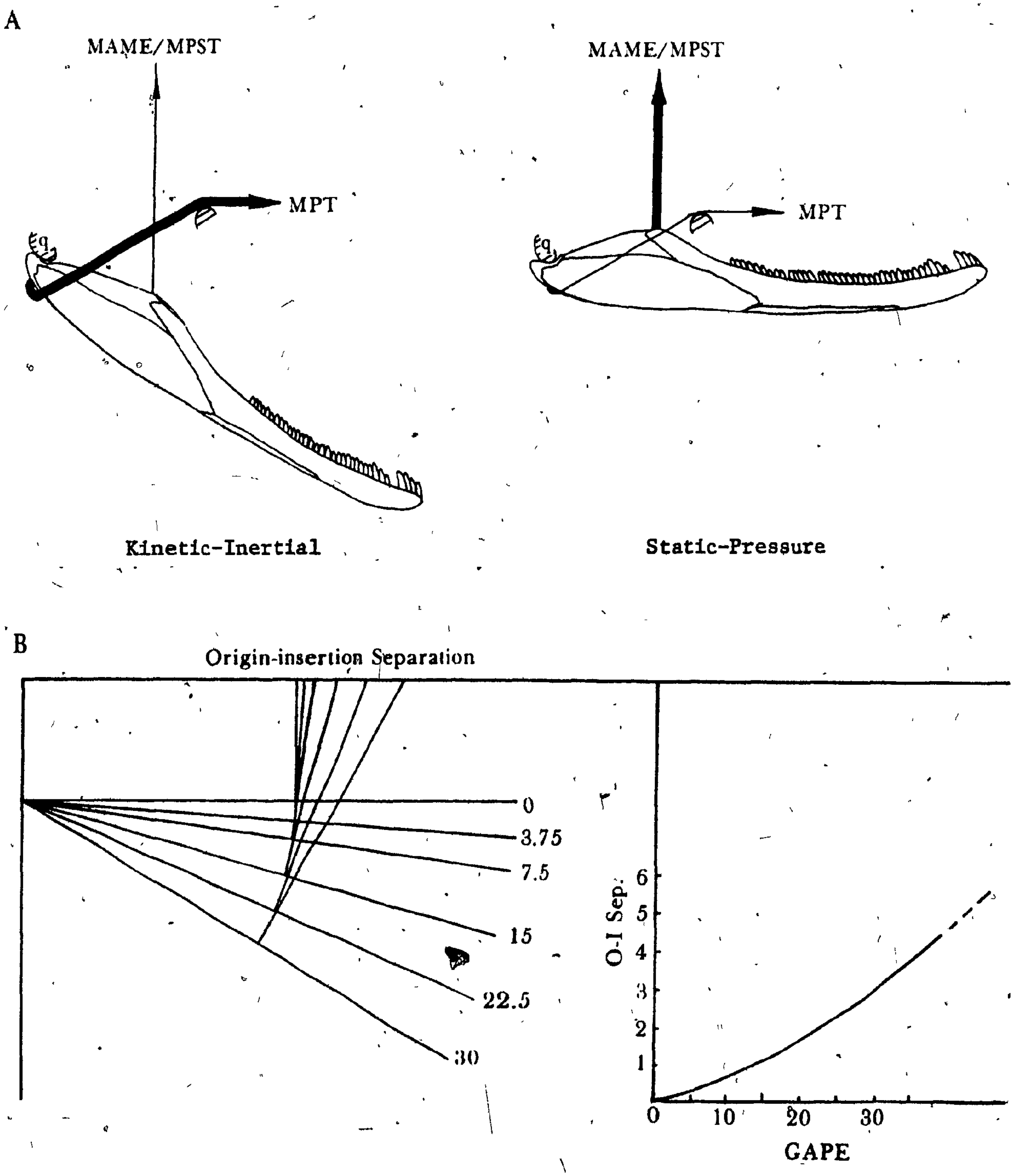


Figure 5. a) Force configuration in Kinetic-Inertial and Static-Pressure mandibular adduction systems. b) Maximum gape *vs.* distance between adductor muscle origin and mandibular articulation.

radius (Fig. 5b). It is in this way that the maximum gape can be estimated. Olson believed that the kinetic-inertial system, in which maximum adductor power was transmitted to the depressed mandible by a large anterior adductor (M. adductor mandibulae internus segments) with its origin far forward of the insertion, was primitive to rhipidistan fish and their early tetrapod descendants. He considered the static-pressure system, in which maximum adductor power was transmitted to a fully adducted mandible by a large posterior adductor (M. adductor mandibulae externus et posterior) to be a derived condition typical of most reptiles. He believed that some reptiles, particularly the aquatic crocodilians had a secondarily derived kinetic-inertial mandibular adductor system. While the recognition of these two types of mechanical systems is useful in analysing the functional mechanics of mandibular action, it must be emphasized that the two systems are not mutually exclusive. Many early, generalized reptiles such as the captorhinomorphs had both a kinetic-inertial and a static-pressure system that were well developed rather than a predominant static pressure system as Olson has implied.

Because of a lack of data on cranial kinesis even in modern reptiles, the reconstruction of the metakinetic mechanism and its function in primitive reptiles must be based on a strictly mechanical analysis. The physical parameters of moment arms in cranial lever systems and elasticity and elongation-contraction in adductor muscles can be estimated with reasonable precision and, thus, would have limited the responses that might potentially be expected. Even Frazzetta's (1962) important paper on cranial kinesis in modern lizards followed the same mechanical approach since it is extremely difficult to obtain data on the electrical activity and tensions (passive or active) of individual muscle slips as well as on small scale movements of the skull segments even in living forms. Nevertheless, an attempt must be made even in the presence of formidable obstacles to gain an understanding of this extremely important mechanism. It is hoped that as new information on muscle physiology, cranial kinesis, and behaviour in modern reptiles becomes available that a more refined explanation of the functional mechanics of fossil reptiles can be produced.

Electromyographic studies of vertebrate, and in particular mammalian, musculature are relatively common (Basmajian, 1967; Gans, 1974) and provide much of the basis for our understanding of the processes of muscle excitation and contraction. The electrical activity of reptilian musculature, especially cranial musculature, has only just begun to be studied (Rieppel, personal communication). A large number of background action potentials are recorded from muscle tissue throughout its range of movement and activity. In general, however, there is a greater degree of excitation recorded above the background when the muscle is actively contracting that when it is at rest with maximum excitation occurring at the point of greatest applied power. Muscle fiber-tendon lengths and bone ossification and development are sufficiently plastic within individuals that natural optimisation of mechanical systems will always occur (Haines, 1932, 1934; Washburn, 1946, 1947). As a result, conclusions as to the mechanical efficiency and function of a simple dynamic system with only one or two moving parts and operating in only one plane can be made with a reasonable degree of confidence.

A muscle fiber when at rest has a single fixed length (resting fiber length). If excited that fiber will exert its greatest force as it begins its contraction. As contraction progresses, the power that the muscle fiber can exert diminishes until the point of complete contraction, about 65 to 70 percent of the resting fiber length, is reached (Fig. 6). Elongation of the muscle fiber by an external load is resisted by an active tension that decreases with elongation and a passive (elastic) tension that increases to allow a maximum elongation of about 130 to 135 percent of the resting fiber length before the sarcolemma begins to tear (Zierler, 1961; Gordon, Huxley, and Julian, 1966). It is obvious that maximum gape must be achieved without any segments being elongated beyond the critical 130 percent elongation beyond the resting fiber length. If all of the muscle segments pass through their full contraction range during the adduction cycle, the common elongation factor may be eliminated and the time required for that elongation to proceed substituted and the speeds of contraction of individual segments compared. The cascading effect of the different muscle divisions and subdivisions reaching their resting fiber lengths at different times maintains the near constant total power curve as illustrated in Fig. 7.

CRANIAL KINESIS IN PRIMITIVE CAPTORHINOMORPH REPTILES

The adduction-depression cycle of jaw movement can be divided into six distinct stages, each characterized by specific relationships between the maxillary and mandibular segments and between the maxillary and occipital segments. The first stage of analysis consists of an examination of movements in the vertical plane only, with the braincase and neck held horizontally by the cervical musculature. Even in the analysis of cranial kinesis in small primitive captorhinomorphs, gravity must be recognized as a significant force typically acting in the sagittal plane.

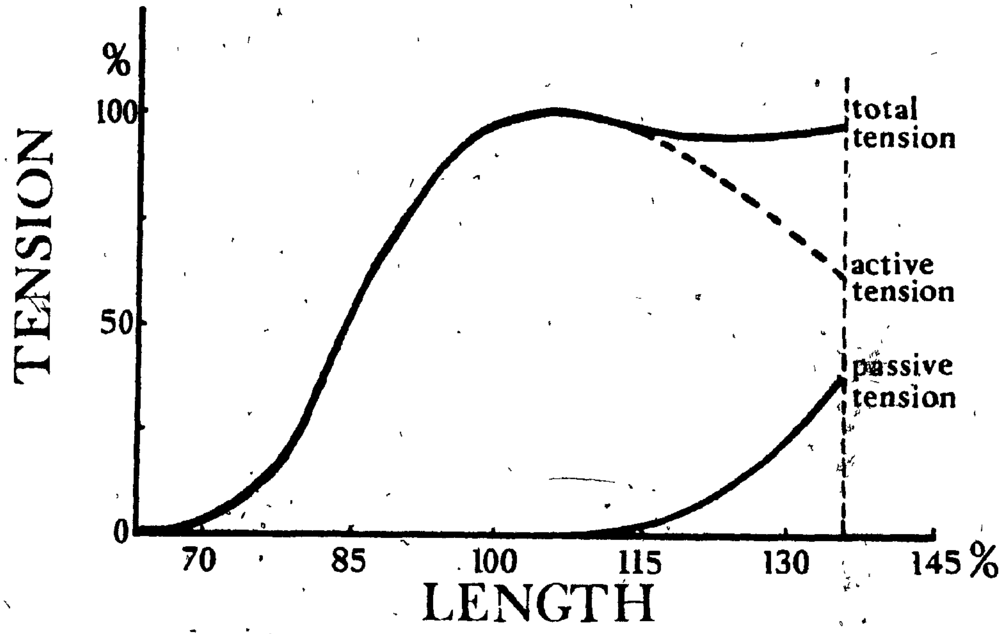


Figure 6. Muscle Tension-Elongation Curve (after Zierler 1961).

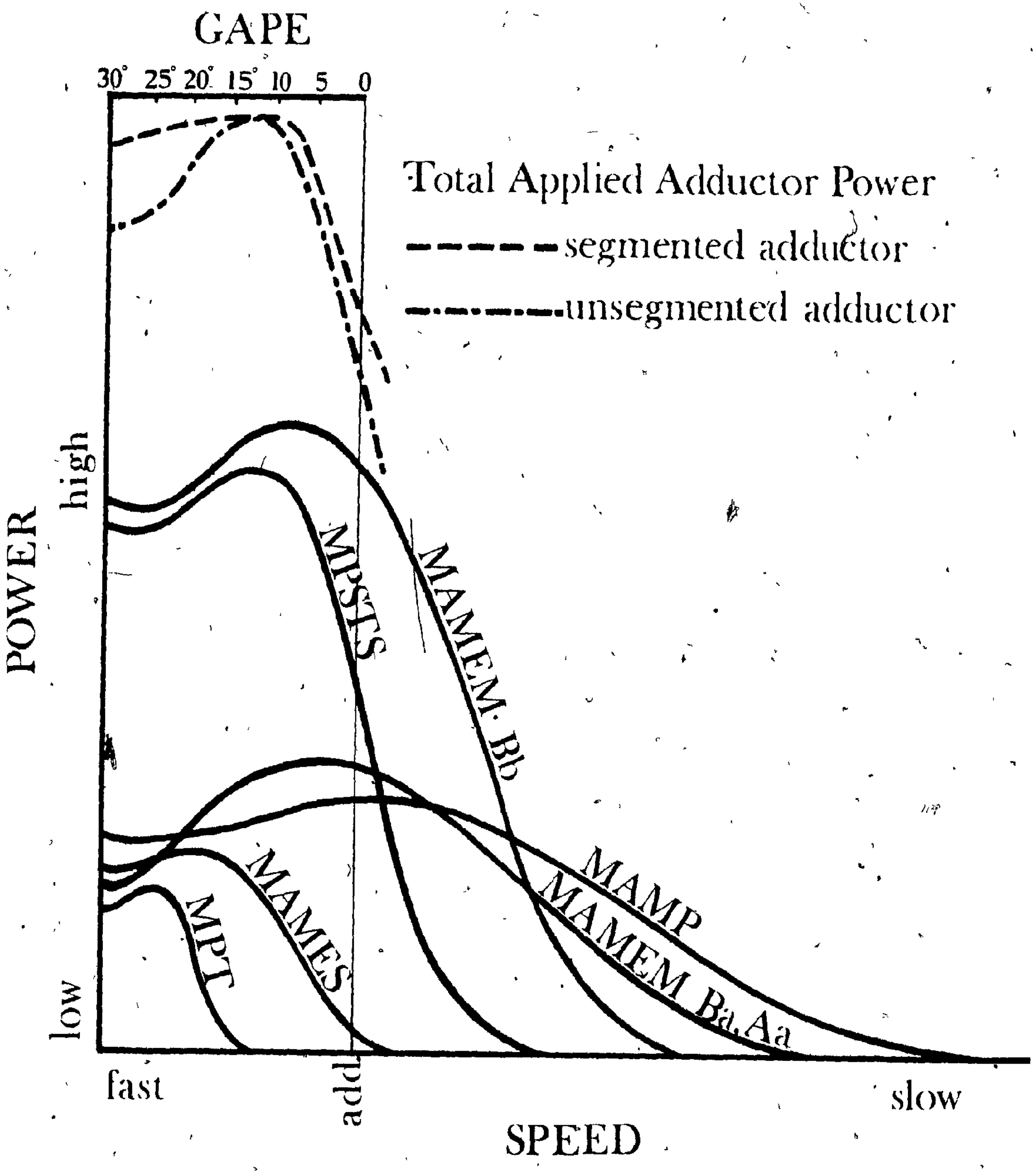


Figure 7. Hypothetical cascading of resting fiber lengths of mandibular adductor muscles during adduction cycle.

Resting Position

The so-called resting position with the skull roof lowered and the jaw adducted is, in reality, a misnomer since the force of gravity acting upon the maxillary, occipital, and mandibular segments must have been countered by various different muscular forces, either internal (elastic) or external (stimulated) (Fig. 8a). Gravitational and adductive forces kept the skull roof lowered relative to the braincase as they do in modern metakinetic reptiles. Gravitational forces were transmitted to the occipital segment from the maxillary and mandibular segments through some of the adductor musculature, through the supraoccipital and basipterygoid articulations and, to a lesser extent, through the paroccipital processes. Interestingly, the basipterygoid articulation lay immediately ventral to the apparent centre of gravity of the head in contrast to the condition seen in modern *Sphenodon* and lizards where the articulation lies much further posteriorly. In captorhinomorphs the epipterygoid was large and roofed the epipterygoid recess, thus allowing transmission of gravitational forces to the basipterygoid processes. Since the metakinetic axis in primitive captorhinomorphs was along the contact between the postparietals and the supraoccipital rather than between the paroccipital processes and the squamosal and quadrate as in *Sphenodon* and most lizards, an anteroposterior compressive force couple existed between the epipterygoid and the basicranial tubercle in addition to the typical dorsoventral force couple (Fig. 9). In *Sphenodon* and lizards in which metakinesis is not well developed, an anteroposterior, gravity induced, compressive force couple between the pterygoid (the epipterygoid is secondarily reduced) and the basipterygoid tubercle has been greatly reduced or eliminated because

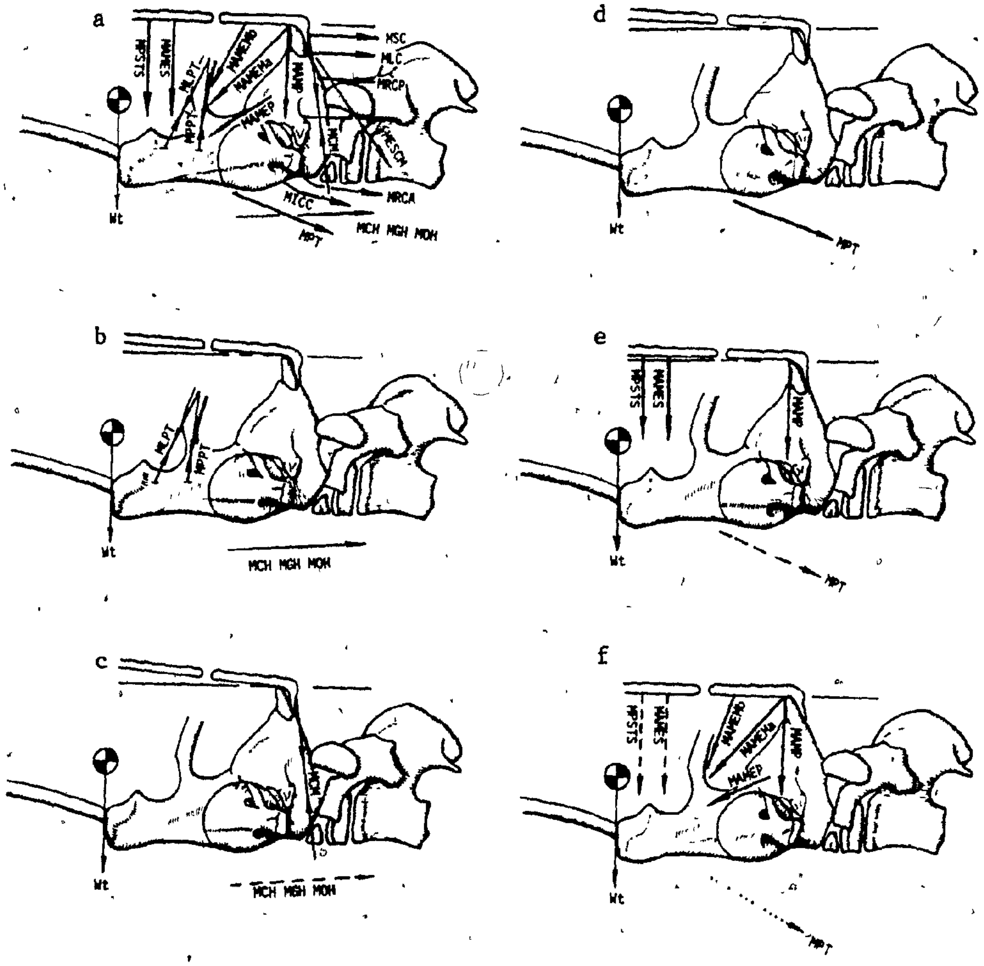


Figure 8. Schematic diagram of metakinetic movments during a complete mandibular depression-adduction cycle. a) All forces acting upon the skull. b) Beginning of mandibular depression cycle. c) End of mandibular depression cycle. d) Beginning of mandibular adduction cycle. e) Middle of mandibular adduction cycle. f) End of mandibular adduction cycle. Solid lines: beginning of contraction. Dashed lines: maximum active contraction. Dotted line: end of active contraction.

the basicranial articulation lies in the same plane as the metakinetic axis, normal to the line of action of the gravitational force. As a result of the anteroposterior force couple in primitive captorhinomorph reptiles, the basicranial articulation consisted of a deep, heavily reinforced socket into which the robust basipterygoid tubercle fit. This was similar to the form of basicranial articulation seen in *Sphenodon* but quite different from the lightly built sliding articulation in lizards.

It is believed that the mandibular segment in all reptiles does not require significant active muscular forces, beyond background excitation, to keep it adducted. All muscles have a specific resting length of muscle fiber from which a maximum of about 30 to 35 percent total elongation or shortening is possible (Zierler, 1961; Barghusen, 1968). In most cases the resting fiber length is thought to occur when the mandible is partially depressed. In only a few cases is the resting fiber length believed to be reached when the mandible is fully adducted. Because of these limits on total elongation and contraction, muscles that reach their resting fiber length at the point of full adduction must be so constructed or positioned that elongation at full mandibular depression does not exceed the 30 to 35 percent maximum (Fig. 7). This can only be accomplished in two ways. Since circumferential extension at a given angular displacement of the jaw varies directly as the length of the moment arm between the articulation and the origin or insertion, a muscle originating well anteriorly on the skull roof or braincase, or inserting far anteriorly on the mandible must have exceedingly long muscle fibers in order for the total elongation of the muscle to remain less than the maximum allowable 30 to 35 percent total resting fiber length. This is a system that is present in both chamaeleonid lizards (Poglayen Neuwall, 1954; Haas, 1973) and ceratopsian dinosaurs (Haas, 1955; Ostrom, 1964) where the frill supported M. adductor mandibulae externus profundus is greatly elongated, but otherwise is extremely rare. In anapsid captorhinomorphs such an approach was impossible so that an alternate arrangement developed. In captorhinomorphs, the musculature inserted close to the articulation, thus greatly decreasing the circumferential extension. This musculature apparently consisted of the large M. adductor mandibulae externus profundus that originated on the lateral surface of the supraoccipital and the anterodorsal surface of the prootic and of the smaller M. adductor mandibulae posterior that had its origin on the lateral and anterior faces of the pterygoid lamella and occipital flange, respectively, of the quadrate. The mandible was apparently held adducted by the resting muscles and, hence, the natural elasticity of the muscle fibers, with little physiological effort. There was no need for active stimulation, above background, of the muscles to keep the mandible adducted. Gravitational forces acting upon the mandible were transferred to the braincase and maxillary segment by these muscles.

Beginning of Mandibular Depression

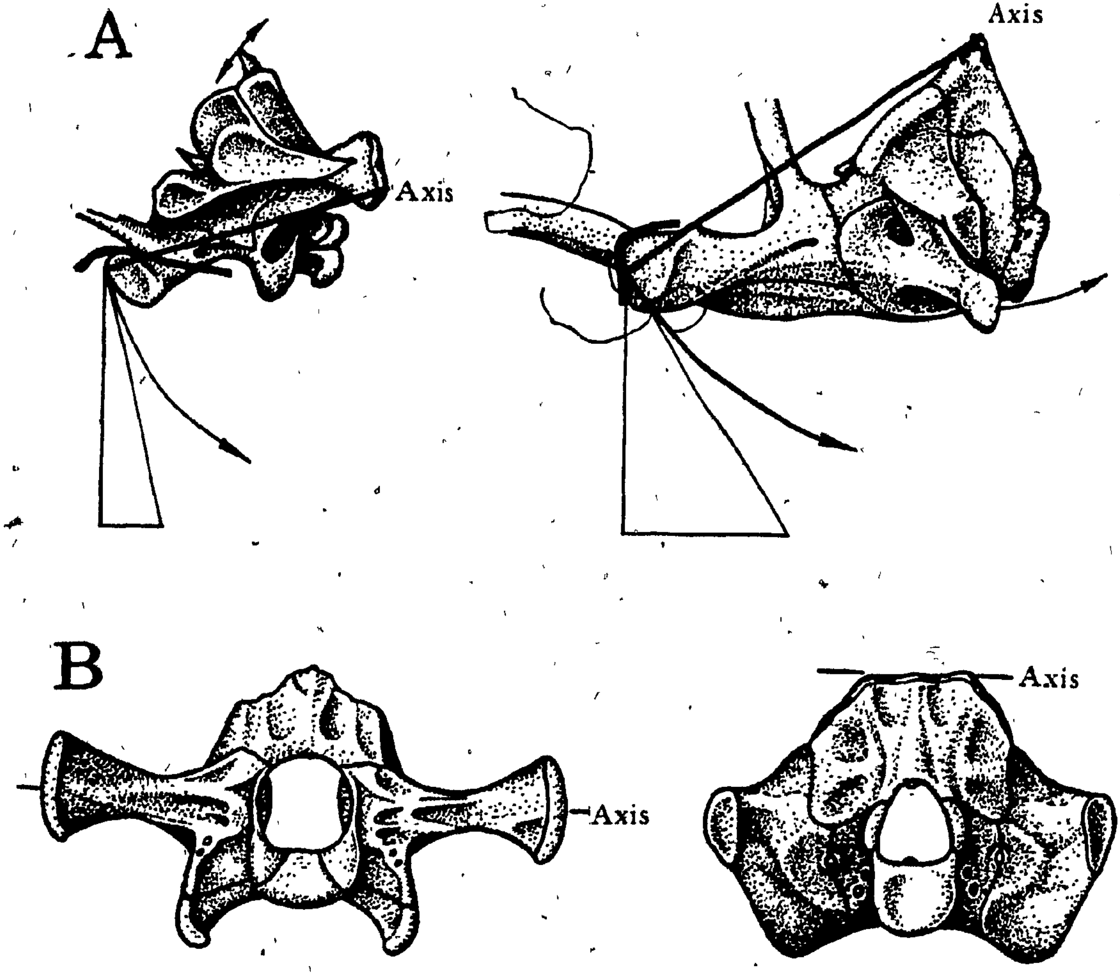
At the beginning of the mandibular depression cycle the mandibular segment was lowered and the maxillary segment raised slightly (Fig. 8b). The principal elevators of the maxillary segment in primitive captorhinomorphs are believed to have been the M. levator pterygoidei and M. protractor pterygoidei divisions of the M. constrictor dorsalis group just as in modern *Sphenodon* and lizards. The levator pterygoidei of captorhinomorphs apparently originated from the lateral surface of the braincase ventral to the M. pseudotemporalis superficialis origin and inserted onto the medial surface of the broad base of the epipterygoid. This is generally similar to the position of the M. levator pterygoidei in the modern rhynchocephalian *Sphenodon* (Lakjer, 1926; Ostrom, 1962; Haas, 1973). In *Sphenodon* the quadrate ramus of the pterygoid is proportionately lower than in captorhinomorphs and the alar process of the prootic greatly expanded anterodorsally. As a result, when present in younger individuals, the M. protractor pterygoidei of *Sphenodon* is relatively long-fibered and is oriented anterodorsally. In captorhinomorphs, the high pterygoid and low alar process of the prootic apparently indicate the former presence of a short-fibered, posterodorsally oriented M. protractor pterygoidei. In *Eocaptorhinus* where metakinesis appears to have been greatly reduced or even lost in adult animals, the M. protractor pterygoidei is thought to have been reduced significantly in size and, perhaps, even lost. This parallels closely the condition seen in *Sphenodon* which is metakinetic as a juvenile, but often is akinetic as an adult (Versluys, 1912b; Ostrom, 1962). It was contraction of the M. levator pterygoidei and possibly the M. protractor pterygoidei that initiated elevation of the maxillary segment (snout, skull roof, and palate) relative to the occipital segment (braincase). The primary antagonist acting against initial elevation of the maxillary segment was the force of gravity. Since only the M. adductor mandibulae posterior and possibly the M. adductor mandibulae externus profundus are thought to have reached their resting fiber length at full mandibular adduction, little if any muscular forces were likely to have acted upon the braincase at the beginning of the mandibular depression cycle.

Mandibular depression was apparently initiated by contraction of the posteriorly directed superficial hyoid musculature, in particular the M. coracohyoideus, M. geniohyoideus, and M. omohyoideus. In primitive captorhinomorphs that had not developed a long retroarticular process, the M. cervicomandibularis apparently inserted too close to the mandibular articulation to have been significant in initiating mandibular depression. Since the hyoid musculature was located well below the articulation, these muscles would have had a significant mechanical advantage during the early stages of mandibular depression thus allowing them to function as the earliest acting mandibular depressors.

Complete Mandibular Depression

As mandibular depression increased toward the maximum gape (Fig. 8c), the various adductor muscles successively reached or passed their resting fiber lengths. The points at which these resting fiber lengths were reached or passed varied from muscle to muscle depending upon the specific function of the muscle in the depression-adduction cycle. The first muscle to pass its resting fiber length is believed to have been the M. adductor mandibulae profundus. Because it did not originate on the braincase, it was not a significant element in cranial metakinesis. Sequentially thereafter, the M. adductor mandibulae externus pars profunda, pars media, pars superficialis, M. pseudotemporalis superficialis and profunda, and finally M. pterygoideus are believed to have reached their resting fiber lengths (Fig. 7). The effect of passive tension in these muscles would be to depress the maxillary segment relative to the occipital segment. These tension forces would have been opposed principally by the M. levator pterygoidei and, to a lesser extent, by the smaller M. protractor pterygoidei, which acted to raise the maxillary segment of the skull relative to the occipital segment.

In *Sphenodon* and many metakinetic lizards, full elevation of the maxillary segment is limited not only by the maximum contracted length of the M. levator pterygoidei and M. protractor pterygoidei (about 65 to 70 percent resting fiber length), but also by physical limits. These consist of the broad lateral ascending processes of the supraoccipital rocking forward to meet the medial descending flange of the parietals or, as in iguanid lizards, the long median ascending process of the supraoccipital rocking forward to the anterior end of the parietal fossa (Fig. 9). Physical limits of this type can only be developed in forms with a low metakinetic axis passing through the paroccipital processes. In primitive captorhinomorph reptiles, where the metakinetic axis lay along the postparietal-supraoccipital junction, physical limits such as have been developed by many modern lepidosaurs, did not exist. Instead, the robust, dorsoventrolaterally inclined stapes served to limit maximum elevation of the maxillary segment. Unlike the condition found in lepidosaurs where the stapedial footplate is suspended by an annular ligament within the fenestra ovalis, captorhinomorphs and many other primitive reptiles had a heavily built stapes whose broad footplate formed a three-dimensional ball-and-socket joint with the lateral wall of the braincase around the small fenestra ovalis (Fig. 10). The true fenestra ovalis "internus" was only about 25 to 30 percent of the diameter of the stapedial footplate in *Eocaptorhinus* (Heaton, 1975, 1978). The distal end of the stapes typically lay within a pronounced columellar or stapedial recess in the quadrate (Carroll, 1969a; Heaton, 1975, 1978) along which it may have been able to slide. It was



Lizard Braincase

Captorhinomorph Braincase

Figure 9. Potential degrees of freedom at basicranial articulation. Position of metakinetic axis.

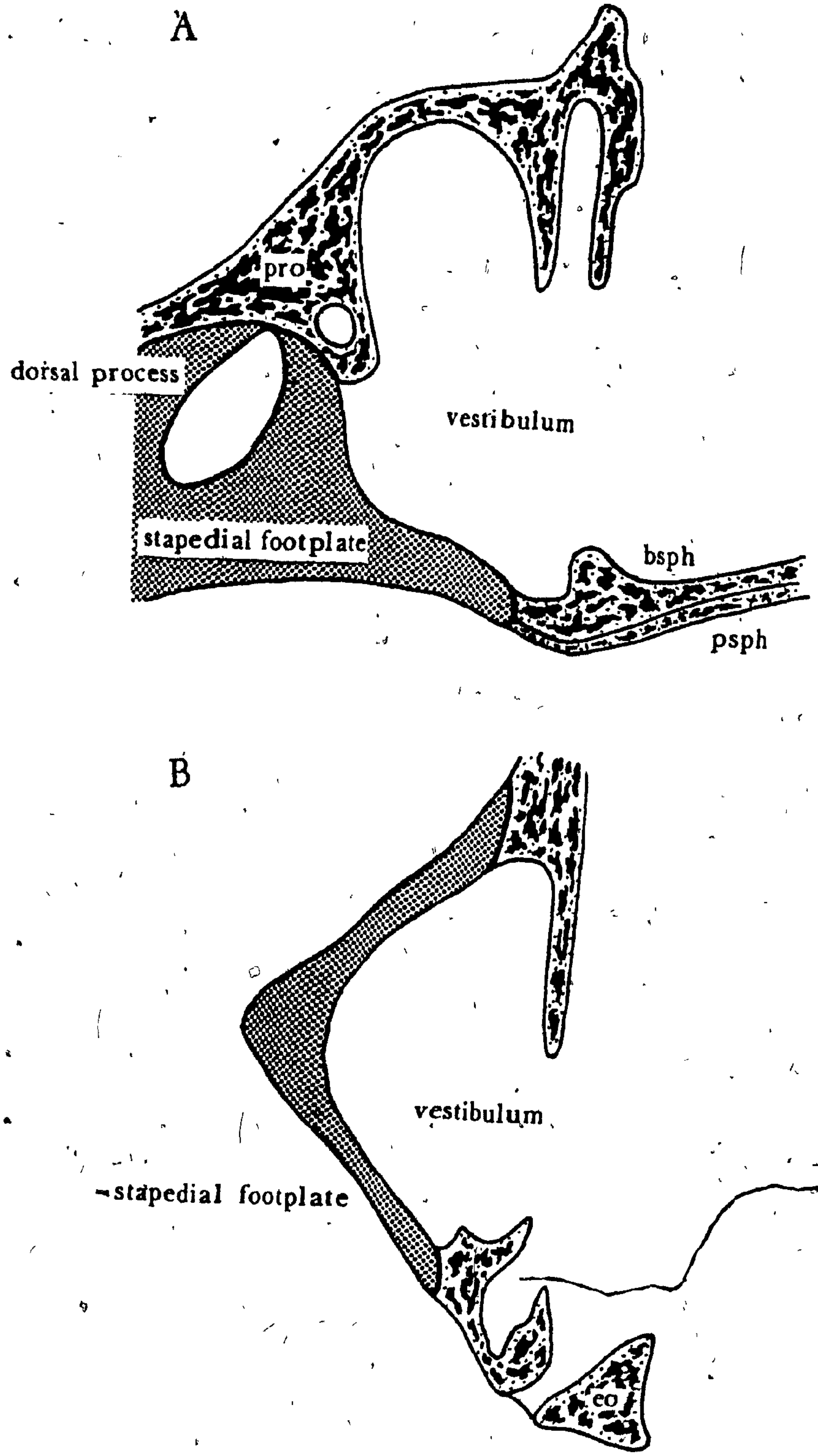


Figure 10. *Eocaptorhinus laticeps*. Section through fenestra ovalis showing ball and socket articulation. a) Transverse section along the columella of the stapes. b) Frontal section ventral to the columella of the stapes.

apparently limited in the extent of its posteroventral movement by both a slight narrowing of the columellar recess and by a small medial lip at the posteroventral end of the recess.

As the power applied by the hyoid musculature to depress the mandible decreased with increased contraction, it is believed that the M. cervicomandibularis (M. depressor mandibulae) began to increase its applied power. Because the mandible of primitive captorhinomorphs did not possess a retroarticular process, the M. cervicomandibularis passed too close to the mandibular articulation, when the jaw was adducted, to gain a significant mechanical advantage during the initial stage of mandibular depression. With the insertion of the M. cervicomandibularis on the posteroventral extremity of the articular well below the mandibular articulation, the M. cervicomandibularis gained a significant mechanical advantage as mandibular depression progressed. This appears to have been an efficient system stressing high speed but relatively low powered action during the early stages of mandibular depression before the resting fiber lengths of the jaw adductor muscles were reached. As the mandibular adductor muscles reached or passed their resting fiber lengths, the eccentric cam action of the posterior extremity of the mandible allowed application of increased power to the mandible by the M. cervicomandibularis to counter increasing passive elastic forces in the adductor muscles. This same basic pattern of attachment of the M. cervicomandibularis has been retained by most synapsid reptiles with some developing a ventral retroarticular process to increase the mechanical advantage of the M. cervicomandibularis at full mandibular depression (Gans, 1966). A large number of reptiles including *Eocaptorhinus*, developed long, posteriorly directed retroarticular processes that greatly increased the amount of power that could be applied to open the mandible both by increasing the mechanical advantage afforded the M. cervicomandibularis and by increasing the area of insertion of that muscle. The development of a long posteriorly directed retroarticular process may be related to the greatly increased mass and, hence, strength of the adductor musculature in forms such as *Eocaptorhinus* and *Captorhinus* and the necessity to increase the power applied to the mandible to stretch these muscles beyond their resting fiber length at which point passive tension would have begun to increase. As Gans (1966) indicated, development of a posteriorly directed retroarticular process would have reduced the maximum gape of these animals considerably. Amongst modern insectivorous lepidosaurs, *Sphenodon*, which lacks a tympanum, has retained the primitive condition with no well developed retroarticular process. Most lizards have a tympanum supported by a deeply recessed quadrate. A long retroarticular process has developed ventral to the tympanum allowing the M. cervicomandibularis to insert onto the articular without impinging upon the tympanum. The selective pressures that have led to the development of posteriorly directed retroarticular processes in many captorhinids and in many lizards appear, therefore, to be unrelated.

Beginning of Mandibular Adduction

The adduction cycle is interpreted as if a uniform, resistant but compressible prey object were held in the mouth. This object would develop a resistance to the adductive forces in accordance with Hooke's Law that "within certain limits the ratio of unit stress to unit strain is constant". Thus, as strain (compression) is increased by decreasing the angle of mandibular depression, stress (internal resistive force) increases linearly.

Since no shearing or tearing of the prey item is likely to have occurred in primitive captorhinomorphs, the teeth having served only to grip it, non-Hookian characteristics associated with the mechanical yield or failure of the prey item need not be considered. While most prey items encountered by primitive captorhinomorphs were not of homogeneous structure and, hence, were non-Hookian in their response to stress, the use of a uniformly compressible solid prey simulation aids in simplifying the explanation of the adductive forces involved. The simulated prey item is assumed to have had a diameter equal to about 50 percent of the distance, measured circumferentially about the mandibuloquadrate articulation, between the maxillary caniniform tooth and the mandibular teeth at an assumed maximum gape of 25 degrees. Under these conditions, no external load was applied to the maxillary, occipital, or mandibular segments during initial adduction.

Mandibular adduction in primitive captorhinomorphs apparently occurred through sequential contraction of many separate jaw muscles just as in modern reptiles. The first muscles to come into play were those forming part of the kinetic-inertial adductor system. The principal muscle of this group was the M. pterygoideus (Fig. 8d). As Haines (1932) has shown, muscles accommodate their resting fiber lengths to the mechanically most efficient position of the elements to which they are attached. Because it originated on the posterodorsal surface and ventral margin of the pterygoid much below the origins of the other adductor muscles, the M. pterygoideus would have reached its most efficient line of action, approaching 90 degrees, only when the mandible was fully depressed (Fig. 5b). It has been assumed, using Haines' observations as a guide, that the resting fiber length of the M. pterygoideus were achieved at this point.

While the origin of the M. pterygoideus, and especially the pars superficialis, was concentrated far from the mandibuloquadrate articulation, the insertion was not. This suggests that the primary function of the M. pterygoideus was as a rapid jaw accelerator in adduction just as the M. cervicomandibularis was in depression, at least in primitive captorhinomorphs (Fig. 7). In contrast to the depression cycle, there was no powerful muscle to initiate rotation of the mandible nor was the force of gravity of assistance. As a result, the M. pterygoideus had to be a massive muscle of much greater cross-section area than the M. cervicomandibularis even though both muscles were acting upon the same mandible within comparable ranges of rotation.

Since contraction of the M. pterygoideus stressed only the maxillary and mandibular segments and not the occipital segment, movement between the braincase and the skull roof did not necessarily occur at this stage.

Partial Mandibular Adduction

After initial acceleration of the mandible by contraction of the massive M. pterygoideus, a second stage of modest sustained adduction force, acting at high contraction speeds was needed to continue to accelerate the mandible. A relatively thin, long-fibered muscle with a wide circumferential operating range was necessary to develop a significant applied force at high speeds. It appears that the M. adductor mandibulae externus superficialis, a thin muscle sheet that originated from the ventral surface of the parietal and inserted on the lateral edge of the lateral surface of the surangular served this purpose (Fig. 8e).

Neither the M. pterygoideus nor the M. adductor mandibulae externus superficialis originated or inserted onto the occipital segment, therefore, contraction of one or both of these elements need not necessarily cause rotation of the maxillary segment relative to the occipital segment. If, as is suspected, the M. levator pterygoidei and M. protractor pterygoidei did not relax until after initial acceleration of the mandible was begun, proportionately little depression of the maxillary segment would have occurred. If the prey item were first contacted by the mandibular dentition, immediate deceleration of the mandibular segment and acceleration of the maxillary segment would occur, within the narrow rotational limits of the maxillary segment, so as to equalize, as nearly as possible the impact forces both dorsal and ventral to the prey item. The reverse would have occurred if the maxillary segment contacted the prey item first. In either case, the effect would have been to minimize the centrifugal force couple by reducing radial acceleration of the prey item before contact by both the maxillary and mandibular dentitions, thereby reducing the chances of the prey item being expelled from the mouth. In addition, this system is believed to have allowed the maxillary caniniform teeth to be accelerated downward into the prey item at the same time as the mandibular teeth are being accelerated upward, similar to what Frazzetta (1962) believed occurred in modern lizards.

Once contact had been made with the prey item, both the maxillary and mandibular segments would have begun to decelerate rapidly. It is believed that the M. pseudotemporalis superficialis, a massive jaw adductor inserting far anteriorly on the basal aponeurosis, began to contract at about this position. Its large cross-section indicates that it was primarily a power adductor, the first contracting element of a static pressure system whose main function was to crush and compress the prey item

(Olson, 1961). The M. pseudotemporalis superficialis is believed to have originated from the lateral surface of the cartilaginous elements (pila antotica, taenia marginalis) of the braincase (chondrocranium) and the anterodorsal edge of the epipterygoid. The attachment to the dorsal ridge of the chondrocranium was apparently a unique feature of primitive reptiles since all later reptiles, wherein the M. pseudotemporalis is large, originate from a descending medial flange of the parietal that has come to sheath the lateral surface of the chondrocranium. Thus, in most modern lepidosaurs and crocodilians, the M. pseudotemporalis superficialis connects the maxillary and mandibular segments of the skull. In primitive reptiles, the dorsal elements of the chondrocranium were undoubtedly part of the maxillary segment and probably were separated from the ossified ventral braincase elements of the occipital segment by a thin flexible postoptic membrane. It appears, therefore, that even though the M. pseudotemporalis superficialis origin appears quite different in primitive reptiles and in modern lepidosaurs and crocodilians, there were few, if any, functional differences.

Soon after the M. pterygoideus superficialis began to contract, the M. adductor mandibulae externus medius Bb apparently started its contraction (Fig. 7). Its function is believed to have been similar to that of the M. pseudotemporalis superficialis, serving as a massive power adductor moving the mandibular segment relative to the maxillary segment. This muscle was apparently quite large in primitive captorhinomorphs and even larger in captorhinids. Its position with both its origin and insertion posterolateral to those of M. pseudotemporalis superficialis suggest that it began its contraction as the active tension in the M. pseudotemporalis superficialis began to decrease rapidly (Fig. 7).

The M. pseudotemporalis profundus was apparently a thin, relatively short-fibered muscle originating from the base of the epipterygoid and inserting on the medial surface of the coronoid. Its exact function is obscure but its ventrolateral orientation suggests that it may have served principally to oppose lateral loads on the mandible rather than as a primary adductor.

The M. intramandibularis was apparently well developed in captorhinomorphs as it is in modern crocodilians and turtles. It appears to have been an accessory adductor giving greater range of length and power to the action of the M. pseudotemporalis superficialis.

Full Mandibular Adduction

As the fully adducted position of the mandible was approached, the M. adductor mandibulae externus pars media Ba, pars media Aa, pars media Ab, pars profunda, and M. adductor mandibulae posterior are believed to have contracted sequentially form front to back (Fig. 7, 8f). The effect of this would have been to maintain a relatively constant force on the mandible throughout the final phase of its adduction. All of these muscles except the M. adductor mandibulae posterior originated from the occipital segment. The contraction of these muscle served to propel the maxillary segment downward, forcing the caniniform teeth into the prey item. There are no maxillary segment depressor muscles directly connecting the maxillary segment and the occipital segment. Instead, an indirect system exists in *Sphenodon* and lizards and, apparently also existed in primitive metakinetic captorhinomorphs, in which muscles originating from the braincase elevate the mandibular segment relative to the occipital segment and muscles originating from the maxillary segment and inserting on the mandibular segment depress the maxillary segment relative to the mandibular segment. As long as the muscles originating from the maxillary segment exert more force than the muscles originating from the occipital segment, the maxillary segment will be depressed relative to the occipital segment. In accordance with the basic assumption that muscle lengths and angles of action were optimized to produce their greatest forces at the mechanically most efficient position, the successively later acting muscles originated more posteriorly and ventrally on the braincase. The most efficient muscle insertion angle (90 degrees) was probably achieved by the M. pseudotemporalis superficialis and M. adductor mandibulae externus medius Bb. Depending upon the degree of arching of the muscle fibers, the M. adductor mandibulae externus partes media Ba and media Ab may also have had insertion angles near 90 degrees when the mandible was depressed between about 10 and 5 degrees. Although the origin of the M. adductor mandibulae externus profundus was low and the proximal fibers oriented almost horizontally, they probably arched over the quadrate ramus of the pterygoid and thence ventrally to an insertion at nearly 90 degrees to the mandible when it was depressed about 5 degrees. The M. adductor mandibulae posterior does not seem to have inserted onto the mandible at anywhere near a right angle. This is thought to indicate that the muscle was not a significant power or speed adductor. Rather, the M. adductor mandibulae posterior appears to have functioned primarily to keep the mandible adducted, when the mouth was empty, without excessive muscle stimulation. This was possible if the muscle reached its resting fiber length when the mandible was fully adducted (Fig. 7). Many of the early acting adductors would have been held in slight passive compression with the only forces counteracted being gravitational forces. The apparent low insertion angle of the M. adductor mandibulae posterior suggests that it may also have served as a stabilizing element preventing or at least limiting anteroposterior movement of the mandibular segment relative to the maxillary segment.

At the point of full depression of the maxillary segment, further movement was prevented by the basicranial articulation.

FUNCTION OF CRANIAL METAKINESIS

Frazzetta (1962) has given an excellent discussion of how cranial kinesis is employed in modern lizards. His work concentrated on the species *Varanus indicus* which is amphikinetic (more than one functioning cranial joint) exhibiting metakinesis, mesokinesis (movement between the frontal and parietal), hypokinesis (movement between the palatine and pterygoid), and streptostyly (anteroposterior movement of the quadrate). Captorhinomorphs had a much simpler meta-monokinetic skull with a single moveable joint between the supraoccipital and the postparietals and, where present, the tabulars. This simplifies the analysis of the kinesis in captorhinomorphs and eliminates many theories on the function of the various types of kinesis that are typically found in lizards.

It has been proposed that cranial metakinesis affords a degree of shock absorbing protection for the braincase during rapid jaw adduction (Crompton, 1955a, b; Bellairs, 1957). As Frazzetta (1962) noted, while this may indeed occur in some lizards, there is no evidence to indicate that this is even a minor factor in the selection for or retention of metakinesis. Since the momentum of the adducted mandible travelling at a constant velocity varies as the cube of the linear size, small size, especially with its attendant thinner, more flexible bone, is in itself a sufficiently good protection against heavy shock loads. In fact, there appears to be a negative correlation between metakinesis and size in primitive reptiles, small forms being kinetic and large forms being akinetic.

The discussion of how gape is affected in amphikinetic lizards is quite complex (Frazzetta, 1962). In meta-monokinetic captorhinomorphs only the mandibuloquadrate joint controls the gape in a simple scissors action. Metakinesis has no effect on the gape.

Frazzetta (1962) investigated the possibility that kinesis, and particularly metakinesis, oriented the gape with respect to the line of sight between the animal and its prey much as Moller (1931) and Bock (1960) have suggested occurs in birds. Frazzetta decided that it was unlikely that this was the reason kinesis developed in lizards since the whole maxillary segment of the skull was mobile during prey capture. This would have meant constant reorientation of the line of sight during mandibular adduction which is the opposite of the hoped for result of developing cranial kinesis.

The usefulness of gape orientation in synchronizing maxillary and mandibular impact on a prey item was not discussed by Frazzetta (1962). In the case of the mandibular segment striking the prey item first, the inertia of the prey was probably not sufficient to have provided a strong enough antagonistic force to impale the prey with the mandibular teeth. This is thought to have been the case with many small terrestrial insectivorous tetrapods. In akinetic forms, the mandibular segment, after contacting the prey item would have imparted a tangential acceleration, about the mandibuloquadrate articulation, with a significant centrifugal or radial force component that would have tended to expell the prey item from the mouth. There was a significant selective advantage to reducing the tangential acceleration of the prey item. This was acconplished with the development of metakinesis. As already noted, by having the tooth-bearing segments free to move rapidly relative to the braincase, it was possible for the tooth-bearing segment first contacting the prey item (in this instance the mandibular segment) to decelerate quickly and transfer the applied force to the acceleration of the mandibular segment to drive the caniniform teeth down into the prey item. A similar pattern would have been followed in reverse if the mandibular segment contacted the prey item first.

Metakinesis is not present in all small terrestrial insectivorous lower tetrapods. In these other groups selective pressures acting upon different parts of the animal have produced structures that served as effectively to catch and hold active prey. Such diverse groups as frogs, salamanders, and chamaeleonid lizards employ a sticky tongue to capture prey and use the usually quite small teeth only for gripping the prey after capture. A number of primitive amphibian groups including some microsaurs and dissorophids may have employed a primitive form of tongue-feeding (Carroll, personal communication) thus allowing them to compete successfully with early reptiles.

EMBRYOLOGICAL DEVELOPMENT OF METAKINESIS

The development of metakinesis in reptiles implies a very specialized braincase structure with large unossified regions contributing to marked dorsoventral flexibility. Only part of the braincase including the supraoccipital, exoccipitals, opisthotics, basioccipital, basisphenoid, parasphenoid, and occasionally the interorbital septum or presphenoid was ossified. Reptiles with ossified interorbital septa were akinetic. In modern lepidosaurs the metakinetic axis lies along the axis of the paroccipital process but in captorhinomorphs it lay along the junction between the supraoccipital and the postparietals and, when present, the tabulars. The supraoccipital is formed as an ossification of the embryonic tectum posterior, which lies posterior to the embryonic fissura metotica (Rice, 1920; Goodrich, 1930) not from the tectum synoticum as proposed by Gaupp (1900, 1905), de Beer (1926, 1930, 1937) and Romer (1956) (Fig. 11). In fact, it is the lack of a heavy tectum synoticum anterior to the embryonic fissura metotica, either cartilaginous as in crossopterygians (Romer, 1937, 1941; Eaton, 1939; Westoll, 1943; Jarvik, 1954; Thomson, 1966a, b) or ossified as in labyrinthodont amphibians (Sawin, 1941; Romer and Witter, 1942; Panchen, 1964, 1970, 1972b), that has given the flexibility to the chondrocranium of reptiles. It is believed that were the tectum synoticum present as an embryonic cartilage in akinetic primitive pelycosaurs, pareiasaurs, and true cotylosaurs (diadectids, tseajaiids, limnoscelids, and possibly seymouriamorphs), it would have ossified, as it did in labyrinthodonts, in order to strengthen the skull. The region dorsal to the otic capsules that is heavily ossified in labyrinthodont amphibians and even some modern frogs (Hylidae, some Leptodactylidae, Baldauf, 1963)

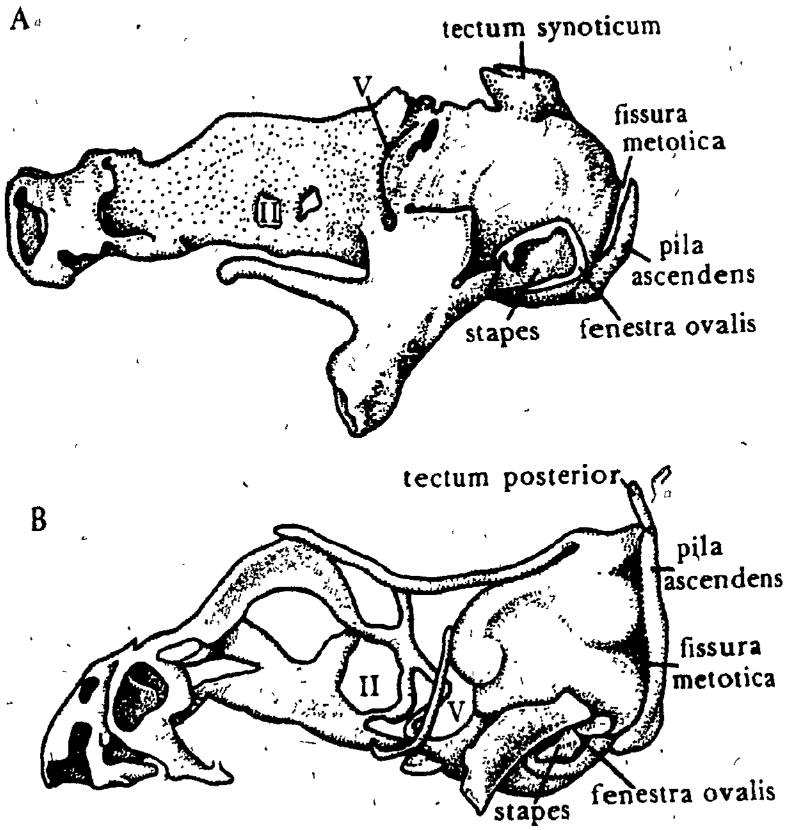


Figure 11. Embryonic chondrocrania. a) Amphibian - the primitive salamander *Hynobius*. Lateral aspect. (from Sehmalhausen 1968 after Regel 1963). b) Reptile - the lizard *Lacerta* (modified after Gaupp 1900).

exists in reptiles only as thin membrane (postoptic membrane) and a narrow cartilaginous taenia marginalis the latter of which is not present in amphibians. The pila antotica of reptiles is a narrow cartilage that bows laterally when compressed during depression of the skull roof. In labyrinthodont amphibians, the pila antotica was a broad heavily ossified plate that formed the dorsal border of the incisura prootic (trigeminal notch) and was sutured to the ossified tectum synoticum. In reptiles, the incisura prootica is open dorsally.

The sphenethmoid region of the braincase of both labyrinthodont and at least some lepospondyl amphibians was a heavily ossified structure (Sawin, 1941; Romer and Witter, 1943; Romer, 1965; Panchen, 1968, 1972b; Carroll and Currie, 1975) composed of several parallel tubes of triangular cross-section. The sphenethmoid region of reptiles is much more simply constructed. It consists of the thin vertical, median, cartilaginous interorbital septum topped by the slightly bowed, paired solum (planum) supraseptale which together have an approximately "Y"-shaped cross-section anterior to the optic foramen and the paired pila metotica and possibly taenia parietalis posteriorly. This type of structure is typically seen in metakinetic modern *Sphenodon* (Howes and Swinnerton, 1901; Save-Soderbergh, 1946) and lizards (Gaupp, 1900; Rice, 1920) as well as in turtles (Rathke, 1848; Kunkel, 1912) and crocodilians (Rathke, 1866; Shiino, 1914), forms that are, today, akinetic. In a few early akinetic reptiles such as adult *Eocaptorhinus*, pelycosaurs, and pareiasaurs, the sphenethmoid region may be heavily ossified as the presphenoid.

In general, compression of the braincase in primitive metakinetic reptiles was compensated by slight lateral bowing of the solum supraseptale, pila metoptica, pila antotica, and their associated metoptic, postoptic, and possibly epioptic membranes. There appears to have been no such allowance for flexibility and, hence, no metakinesis in the braincase of true labyrinthodonts.

IDENTIFICATION OF METAKINESIS IN FOSSILS

The presence or absence of metakinesis in the skulls of primitive reptiles can be determined by examining the degree of ossification of the embryonic chondrocranium. The primary prerequisite is the absence of an ossified, or even thick, cartilaginous, tectum synoticum. Only reptiles and true cotylosaurs (diadectids, tseajaiids, limnoscelids, and possibly seymouriamorphs) have this type of condition; true labyrinthodonts (temnosponyls, anthracosaurs excluding seymouriamorphs) do not. The presence of an unossified solum supraseptale in the sphenethmoid region is also necessary to allow dorsoventral compression of the braincase. This characteristic is usually found only in small lightly ossified forms. Most large primitive reptiles (pelycosaurs, advanced captorhinids, pareiasaurs) and true cotylosaurs had fully ossified sphenethmoid regions. The only groups of primitive reptiles not known to have had ossified sphenethmoids are primitive captorhinomorphs, millerosaurs, and procolophonids, all of which are thought to have been metakinetic (Ivakhnenko, 1973; Gow, 1973) and all the primitive members of which were small. In these three groups of small, potentially metakinetic reptiles, the braincases were not sutured to the skull roofs. The paroccipital processes continued laterally to the quadrate, and occasionally the tabular, as a cartilaginous extension of the opisthotic. The supraoccipital was generally narrow with its dorsal edge generally contacting the ventral surface of the postparietals and tabulars (Fig. 12). In procolophonids, the supraoccipital developed a very lizard-like sliding joint between the supraoccipital and the parietal (Ivakhnenko, 1973). In all of the other groups of primitive reptiles, the supraoccipital was solidly sutured to the skull roof and, with the exception of ophiacodont pelycosaurs, the paroccipital processes sutured to the cheek. This same condition is present amongst the true cotylosaurs except for *Seymouria* in which much of the wide occipital plate was cartilaginous.

In metakinetic reptiles, as noted above, the maxillary and mandibular segments of the skull could only be moved relative to the occipital segment if some of the jaw adductor musculature originated from the braincase. A metakinetic skull indicates a complex mandibular adduction cycle that required a complex system of sequenced muscles such as was present in captorhinomorphs. The simpler adduction cycle in akinetic skulls required a less complex system of adductor muscles. In modern metakinetic lizards and apparently metakinetic captorhinomorphs, the M. adductor mandibulae externus media originates from the anterolateral surface of the supraoccipital, the pars profunda from the lateral edge of the supraoccipital and the dorsal surface of the paroccipital process and bulges posteriorly into the large post-temporal fenestrae. Although the adductor musculature of procolophonids and millerosaurs has not been reconstructed, it is believed to have been generally similar. The development of peculiar lateral temporal fenestrations in the cheeks of some millerosaurs may have permitted the M. adductor mandibulae externus profunda to bulge laterally rather than posteriorly thus allowing medial expansion of the tabulars and squamosals, for increased insertion area of the superficial cervical muculature, to constrict the

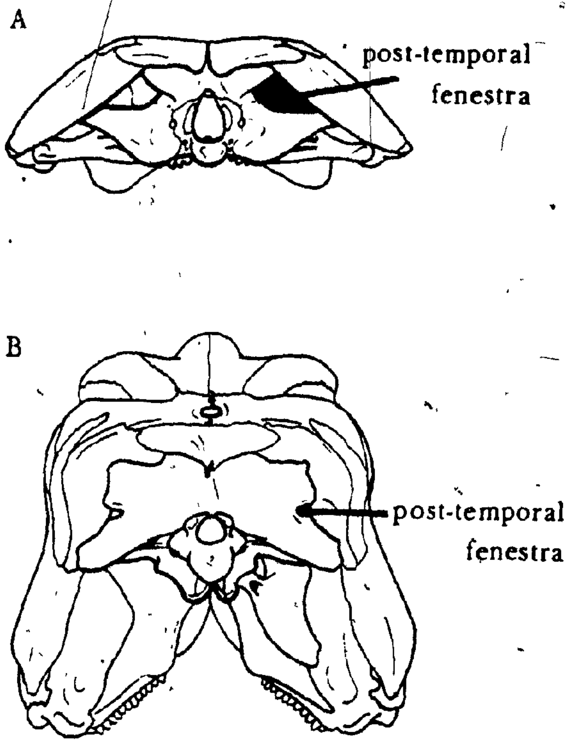


Figure 12. Reptilian occiputs. a) Typical saurian reptile *Eocaptorhinus*. b) Typical synapsid reptile *Dimetrodon* (after Romer and Price 1940).

post-temporal fenestrae slightly.

In akinetic true cotylosaurs, the M. adductor mandibulae externus profunda apparently became reduced and eventually lost, thus allowing the supraoccipital and opisthotic to increase in size to accommodate a large region of origin of the deeper cervical musculature, and causing the post-temporal fenestrae to become greatly constricted and even lost in diadectids. These animals were generally large and very heavily built, requiring powerful muscles to raise the mandible. The M. adductor mandibulae externus medius was probably retained as a major power adductor in true cotylosaurs. The vertical occiput of true cotylosaurs was a primitive character that apparently was retained because of the retention of a large M. adductor mandibulae externus media.

Pelycosaurs, which were akinetic, also show evidence of simplification of the adductor musculature. The restriction of the post-temporal fenestrae had a history similar to that of true cotylosaurs. The occiput of pelycosaurs was, however, steeply sloped anterodorsally rather than vertically as in true cotylosaurs. It is believed that the slope of the occiput in pelycosaurs was a structural modification of the skull after the loss of the M. adductor mandibulae externus medius and its origin on the supraoccipital. The M. adductor mandibulae externus medius could probably be lost only in small, lightly built akinetic forms where the light mandible could be adducted easily by the remaining jaw muscles. The sloped, plate-like occiput with small post-temporal fenestrae in pelycosaurs is, therefore, a reliable indicator of an akinetic skull even in the absence of other evidence.

EVOLUTIONARY IMPLICATIONS

Origin of Reptiles

The existence of metakinesis in primitive reptiles must cast doubt on the currently accepted theory of the origin of reptiles from akinetic anthracosaurian amphibians. The only amphibian group exhibiting the necessary prerequisite for the development of metakinesis, the absence of an embryonic tectum synoticum in the chondrocranium are the true cotylosaurs (similar to the "Parareptilia" of Olson, 1947) including diadectids, tseajaiids, limnoscelids, and seymouriamorphs (sensu stricto). Many of these animals have been referred to the Anthracosauria on the basis of assumed similarities in the structure of the teeth, skull roof, and vertebrae. It is now recognized that phylogenies, and the establishment of relationships, must be based upon the possession of shared derived characters (specializations), not primitive characters. In this case, teeth with labyrinthine infolding of the enamel, as are present in seymouriamorphs, are primitive characters inherited from their remote crossopterygian fish ancestors and should not be used to ally this group with the Labyrinthodontia. Panchen (1972a) has indicated that the pattern of skull roof elements wherein the tabular and parietal are in direct sutural contact and which is regarded as being "anthracosaurian" (Romer, 1947, 1967) is probably the primitive pattern amongst amphibians rather than the derived condition as Romer thought. Romer (1947) modified Watson's (1919) theory of amphibian vertebral element evolution to derive the reptiliamorph (reptilian-true cotylosaur) and the embolomerous (anthracosaurian - sensu stricto) vertebral pattern from a rhachitomous pattern. Recent discoveries of protoreptilian vertebrae in early, primitive dendrerpetontid temnospodyls (Holmes and Carroll, 1977) and gephyrostegid anthracosaurs (Carroll, 1969b, c) has invalidated the Romer-Watson theory and has led Panchen to recognize the protoreptilian vertebral pattern, with its large pleurocentrum and small crescentic intercentrum, as the probable primitive amphibian vertebral type. It is apparent that anthracosaurs have numerous specialized, derived characters, particularly in the structure of the braincase, middle ear, vertebrae, and forelimb structure that distinguish them from the true cotylosaurs and reptiles with quite different specialized, derived characters also in the braincase, middle ear, vertebrae, and forelimb structure.

Although the reptiles and true cotylosaurs shared such specialized, derived characters as the loss of the tectum synoticum and its ossifications, vertebrae, and forelimb structure, all known true cotylosaurs appear too late in the fossil record and are too specialized to have given rise to reptiles. That reptiles and true cotylosaurs are closely related seems certain. It is even possible that a common ancestor, that could have given rise to both groups, would be identified as a true cotylosaur.

The amphibian-reptile transition was characterized by the change in the reproductive cycle from an anamniotic egg to an amniotic egg. As Carroll (1970) has indicated, an intermediate stage of an anamniotic egg laid on land was necessary between a primitive, anamniotic egg laid in fresh water and an advanced, amniotic egg laid on land. The maximum size of an anamniotic egg laid on land was severely restricted by the surface area to volume ratio that controls both the rate of oxygen-carbon dioxide exchange and the rate of water loss. The maximum diameter of anamniotic egg laid on land by modern plethodontid salamanders is about 7 mm (Salthe, 1969; Carroll, 1970). There is a strong correlation between egg size and maximum adult size in all terrestrial tetrapods that do not undergo metamorphosis after an aquatic juvenile stage. Carroll (1970) showed that it was unlikely that adult amphibians laying terrestrial anamniotic eggs had a snout-vent length exceeding 100 mm. It is also apparent that until all of the embryonic membranes typical of amniotic eggs developed, these "protoreptiles" and their descendants the very first true reptiles, could not have been any larger. This classic application of modern physiological knowledge to a paleontological problem must control all subsequent work on the origin of reptiles.

The consequences of ancestral reptiles having to have undergone a long period of development at a very small size have been enormous. Potential food resources were extremely limited. As Szarski (1962) and Ostrom (1963) have shown for modern lizards, herbivorous feeding strategies are practical only for relatively large reptiles (snout-vent length greater than 250 mm). The only foodstuff capable of supplying sufficient energy quickly enough to small reptiles was apparently animal protein. Most of this is believed to have been supplied by the diverse fauna of small terrestrial invertebrates, most notably insects and arachnids. In fact, most modern lizards that are herbivorous as adults are insectivorous as juveniles.

Competition between these tiny reptilian ancestors and contemporaneous insectivorous labyrinthodonts and lepospondyls was probably fierce. Structures that gave any animal a selective advantage in the capture of small agile invertebrates was strongly favoured. While some amphibians apparently developed tongue feeding to aid in prey capture, a system still seen in modern frogs and salamanders, reptiles developed cranial kinesis.

The many advantages of kinesis, as noted previously, were in part responsible for the enormous radiation of reptiles that soon occurred.

One of the features most closely associated with small size in amphibians and reptiles is the reduced degree of ossification of endochondral elements. Carpal and tarsal elements, limb ends, and portions of the chondrocranium are often unossified. As already noted, the absence of a tectum synoticum is a character of all reptiles and their true cotylosaurian relatives. It is believed that the amphibian ancestors of reptiles were true cotylosaurs or extremely closely related to them and, consequently, also lacked a tectum synoticum. It was the absence of a tectum synoticum that permitted metakinesis to develop. Very small animals in which there was no tectum synoticum and in which some of the cartilages of the chondrocranium, such as the sphenethmoid and the opisthotic, were unossified were preadapted for a metakinetic condition. In these animals the contact between the supraoccipital and the skull roof was narrow and, considering the light weight of the skull, was probably slightly flexible. Slight passive movement of the braincase relative to the skull roof was possible. Muscles of the M. constrictor dorsalis group (M. levator patatoquadrati of rhipidistian crossopterygians, Thomson, 1966, 1967,; Panchen, 1970) were present in many amphibians (Panchen, 1964) including the ancestors of reptiles. These permitted active elevation of the maxillary segment right from the first occurrence of metakinesis.

In rhipidistians the paroccipital process extended laterally leaving a large open fossa bridgei (post-temporal fenestra) (Jarvik, 1954, 1975) within which segments of the mandibular adductor musculature apparently inserted. The pterygoid was low enough and close enough to the braincase to allow these muscle segments to stretch over it dorsally. This arrangement was retained in reptiles and their ancestors, possibly because the relatively large size of the semicircular canals of the inner ear did not permit the paroccipital processes to migrate dorsally and become sutured to the skull roof as they did in the large labyrinthodonts (Carroll, 1970). The access of the adductor muscles to the braincase is critical to the development of metakinesis for it is the muscles originating from it that are able to accelerate the skull roof downward into a prey item. In labyrinthodonts, the large epipterygoid and high pterygoid (Sawin, 1941; Romer and Witter, 1943; Panchen, 1964, 1970, 1972b) prevented the mandibular adductor muscles from originating from the braincase as did the closing of the fossa bridgei.

As a result of the attainment of cranial metakinesis during the passage of the immediate ancestors of reptiles through a stage characterized by extremely small size, a number of cranial osteological characters developed that immediately identify a reptile. A narrow supraoccipital with a limited contact dorsally with the skull roof and horizontal paroccipital processes provided an area of origin for the M. adductor mandibulae externus profundus and produced large post-temporal fenestrae that allowed for the bulging of this muscle. The occipital plate was vertical, making room for the origin of the M. adductor mandibulae externus profundus on the anterolateral surface of the supraoccipital.

The Effect of Size on Metakinesis

While depression of the maxillary segment of the skull relative to the occipital segment was accomplished by several large muscle segments aided by the force of gravity, elevation of the maxillary segment was effected by only two small slips of the M. constrictor dorsalis group, the M. levator pterygoidei and the M. protractor pterygoidei. Strength of bone or muscle tension is directly related to the cross-sectional area of said bone or muscle (a squared function) given a retention of the same proportions while weight, which is dependent upon volume, is a cubic function. It follows that the M. levator pterygoidei and M. protractor pterygoidei were better able to elevate the maxillary segment in a small animal than in a large one. Among primitive anapsid reptiles with massively built skulls, a critical weight seems to have been reached in animals with skulls with a length of about 70 mm as adults. As a result *Eocaptorhinus* with an adult skull length of about 75 to 85 mm was akinetic, as were all adult pelycosaurs, none of which are known to have had skulls of less than 75 mm.

The captorhinomorph family Captorhinidae exhibits a well documented increase in skull size through time. As already mentioned, the earliest captorhinid *Romeria*, with a skull length of 52 to 57 mm was metakinetic. The next oldest form *Protocaptorhinus (=Puercosaurus?) pricei* had a skull of about the same length and also seems to have been metakinetic. The next form to appear was a new (unnamed) species of *Protocaptorhinus (=Puercosaurus?)* 121 mm long which, although the only good specimen is badly crushed, has been preserved with the braincase in place and appears to have been akinetic as an adult as was its contemporary *Eocaptorhinus*.

Labidosaurus, with a skull length of about 250 mm, apparently a direct descendant of the new species of *Protocaptorhinus* (=*Puercosaurus?*), was akinetic as was the even larger and younger genus *Labidosaurikos* (Stovall, 1950) which had a skull length of 300 mm.

In the captorhinid *Eocaptorhinus*, the braincase was stabilized by the anterior extension of the median ascending process of the supraoccipital. The long, heavily ossified stapes formed a solid brace between the lateral surface of the braincase and the deep columellar recess of the quadrate but it was not sutured to either. The median ascending process of the supraoccipital was firmly sutured to the ventral surface of the parietal in *Labidosaurus* while the anterior edge of the footplate of the stapes was sutured to the basisphenoid. The same condition existed in *Labidosaurikos* with additional buttressing of the braincase against the cheek by the paroccipital process and by the stapes which wrapped around its anterodorsal edge. The stapes had become sutured to the prootic around the base of the footplate and dorsal process as well as along the paroccipital process.

Strongly correlated with the loss of metakinesis during the evolutionary history of the captorhinids was the progressive reduction in the size and importance of the caniniform teeth. Accompanying the general increase in size was a significant change in dental characters culminating in the unusual multi-rowed tooth sets of such advanced captorhinids as *Labidosaurikos* (Stovall, 1950), *Rothianiscus* (Olson and Beerbower, 1953), and *Moradiosaurus* (Taquet, 1969). It is obvious that food sources and feeding regimes changed radically during the evolution of the captorhinids possibly culminating in an herbivorous feeding strategy. With the loss of metakinesis and the change from invertebrate food sources, there was apparently a slight selective advantage toward reducing the caniniform tooth. Such a correlation between loss of metakinesis and the reduction of the caniniform teeth in captorhinids is very apparent.

Relationships of the Procolophonoids and Pareiasaurs

Two groups of primitive reptiles, the procolophonoids and the pareiasaurs have had a checkered systematic history. They have often been grouped together as a separate suborder within the poorly understood group of primitive reptiles identified by the much abused term "Cotylosauria" (Romer, 1956, 1967). These two groups exhibit few if any shared derived characters. The main features that appear to unite these two groups seem to be early expansion into a different geographic range, late appearance in the fossil record, and a general dissimilarity to captorhinomorphs. The two groups are probably no more closely related to each other than either is to captorhinomorphs. In fact, there is no general concensus that these two groups are true reptiles. Some most notably (Olson, 1947) have referred to them as the "Parareptilia".

It does appear that both procolophonoids and pareiasaurs had metakinetic ancestors and were, thus, true albeit very primitive reptiles. Primitive procolophonids such as *Tichvinskia vjatkensis* have been shown to be metakinetic (Ivakhnenko, 1973) a fact that could have been surmised by the narrow supraoccipital, large post-temporal fenestra, vertical occiput, and apparently unossified interorbital septum. All known pareiasaurs were akinetic with the supraoccipital sutured solidly to the skull roof and the paroccipital process to the quadrate (Watson, 1914; Romer, 1956). It is apparent that early in pareiasaur history they were metakinetic for they have retained the narrow supraoccipital, large post-temporal fenestrae and vertical occiput of their metakinetic ancestors. The loss of metakinesis appears to have been directly related to large size.

Relationships of Pelycosaurs

The pelycosaurs were the primitive reptiles that first invaded the large terrestrial carnivore and herbivore niches. They are characterized by relatively large adult size and akinetic skulls with wide supraoccipitals, small post-temporal fenestrae, and anterodorsally inclined plate-like occiputs. It is believed that the M. adductor mandibulae externus partes media and profunda had been lost by the time pelycosaurs first appeared in the fossil record. The loss of these muscles was probably correlated with the loss of the ancestral, reptilian metakinesis. It would be simple to ascribe the loss of kinesis in pelycosaurs to a general increase in size as occurred in captorhinids and pareiasaurs but is is difficult to see how loss of metakinesis for this reason could lead to the loss of the large power adductors, the M. adductor mandibulae externus partes media and profunda for they were not lost in captorhinids or pareiasaurs. The loss of primitive metakinesis appears to have occurred early in pelycosaurian history when they were still generally quite small. Immobilization of the braincase occurred through the ossification of the presphenoid, and the lateral expansion of the supraoccipital to become sutured to the interparietal and tabular. Primitively, the paroccipital processes were not fully ossified just as they were not in primitive captorhinomorphs (Carroll, 1969a; Carroll and Baird, 1972). Even the relatively late form *Ophiacodon* displays this pattern (Romer and Price, 1940).

The secondary development of akinesis appears to have occurred in response to the development of a more active, opportunistic, possibly omnivorous feeding pattern. A solely insectivorous role had been abandoned under heavy competitive pressures from the rapidly expanding captorhinomorph lineage. An increasingly diverse fauna of small terrestrial amphibians and reptiles provided a potential food source for any group suitably equipped to exploit it. The chitinous exoskeleton of terrestrial arthropods severely restricted the amount of muscle fiber in the body so that, once firmly clasped by the jaws of a primitive reptile, they were effectively immobilized. It is apparent that small arthropods and soft-bodied invertebrates did not possess the inherent strength to stress the primitive reptilian metakinetic skull. Such was not the case with vertebrates. Their generally larger size, rigid skeleton, and much more massive body musculature would have made them much more difficult to subdue. The relatively unsophisticated metakinetic mechanism of primitive reptiles was probably unable to withstand the heavy stresses placed on it by struggling vertebrate prey. Solidification of the braincase and skull was the most efficient way of reducing these stress problems. It is likely that the assumption of carnivorous feeding modes aided by the development of secondary akinesis first appeared only in sub-adult and adult animals and was acquired at a successively earlier age through time as selective pressures favoured general size increase.

Two interrelated events accompanied the development of secondary akinesis in pelycosaurs. As the supraoccipital expanded, its area of attachment ot the skull roof increased and the paroccipital process widened and lengthened, restricting the areas of origin and thus the ultimate size of the M. adductor mandibulae externus partes media and profunda. As a result of the loss of the metakinesis, these muscles were of little use in their original role of maxillary segment depressors. Consequently, the partes media and profunda became progressively reduced. This undoubtedly occurred rapidly since the reduction of these muscles permitted a general shortening of the adductor chamber. As Reisz (1972) has indicated such a shortening of the postorbital region of the skull would have been a tremendous advantage to a carnivore since it would have resulted in a greatly increased maximum gape. By shortening the postorbital region of the skull a need for separate segments of the power adductors was eliminated since the reduced relative distance between the mandibular articulation and the adductor muscle insertions allowed considerable angular excursion of the mandible without undue lengthening of the muscle fibers. This eliminated the need for the cascading of maximum active tension points (resting fiber lengths) of separate muscle segments without significantly decreasing maximum applied power. This allowed a significant increase in adduction speed, all of which were important factors in the development of a carnivorous feeding pattern (Fig. 7).

Ophiacodont and sphenacodont pelycosaurs appear to have conformed closely to this pattern with ophiacodonts retaining a more primitive strategy of feeding on vertebrates that were generally small enough to be swallowed whole. The lack of serrated cutting edges on the teeth of primitive ophiacodonts and the strongly recurved tips of the teeth in *Ophiacodon* itself tend to favour this interpretation. Sphenacodonts are believed to have appeared later, as large terrestrial herbivores developed upon which they apparently fed. The large teeth with serrated anterior and posterior cutting edges were well suited to tearing ingestable pieces of flesh from animals too large to be swallowed whole.

Both edaphosaurian and caseid pelycosaurs have typical pelycosaurian plate-like occiputs with wide supratemporals, and tiny post-temporal fenestrae. It appears that they arose relatively early from the incipient carnivorous pelycosaur lineage after the development of akinesis and the loss of the M. adductor mandibulae externus partes media and profunda. It is thought unlikely that these herbivorous forms would have reduced or lost the powerful partes media dnd profunda if the development of an herbivorous feeding mode had occurred before the loss of metakinesis. Pareiasaurs give an excellent example of what structural changes occurred when a group became herbivorous first and, although they became akinetic, retained the large post-temporal fenestrae, narrow supraoccipital, and M. adductor mandibulae externus partes media and profunda. The obvious implication of this structural pattern is that the ancestors of edaphosaurs and caseiids must have been active carnivores. This idea of having an herbivorous form develop from a carnivore at first seems unlikely until it is realized that both of these feeding strategies are size and energy dependent. Insects did not provide enough useable protein relative to the energy expended in their capture to have supported either large size or high activity in reptiles. Since increased size usually afforded a measure of protection from predators and would have permitted greater efficiency in food gathering, there were significant selective pressures leading to increased size in many groups of early reptiles. Insects undoubtedly formed the major portion of the food supply of juvenile primitive pelycosaurs with vertebrates making an increasingly significant proportion as the animals grew and their energy requirements increased. Competition amongst primitive pelycosaurs, captorhinomorphs, and terrestrial labyrinthodonts and lepospondyls favoured exploitation of any potential food resource. The one food resource not exploited by either reptiles or amphibians was the abundant terrestrial plant material readily available at that time. While it is unlikely that adult carnivorous pelycosaurs would exploit this resource, their basically insectivorous juveniles might, particularly in periods of extreme competitive pressure. Ostrom (1963) has suggested how primitive insectivorous lizards might have ingested plant material accidentally at first then, with increasing frequency, began to include more and more plant material in their diet as a result of selection for the more efficient exploitation of a new food resource. It is believed that selection amongst the insectivorous juveniles of primitive ophiacodont-like pelycosaurs, the adults of which were carnivorous, led to a similar development of an herbivorous feeding strategy. The exploitation of this enormous food resource at a low energetic cost permitted the development of large size in these early herbivorous pelycosaurs.

Cranial Kinesis and Hearing

In primitive reptiles excessive elevation of the maxillary segment of the skull relative to the occipital segment was prevented by the massive posteroventrolaterally directed stapes. The large stapedial footplate inserted into a socket in the lateral surface of the braincase at the junction of the basisphenoid, parasphenoid, basioccipital, and prootic. This socket, in the captorhinid captorhinomorph *Eocaptorhinus* appears to have been lined with an articulating cartilage suggesting that it may have been a synovial joint. A small fenestra ovalis "interna" with an area of about 25 to 30 percent of the area of the socket (fenestra ovalis "externa") was located within the socket. The rounded edge of the base of the footplate of the stapes indicates that the stapes could rotate about its axis as well as rock slightly. The stapes does not appear to have been capable of any longitudinal movement along its axis as is possible in the stapes of modern reptiles. The stapes of pelycosaurs was generally similar except that the socket was normally ridged to prevent rotation of the stapes. It appears that the solid stapes-braincase abutment was a primitive reptilian character. The distal end of the stapes in *Eocaptorhinus* was held tightly within a deep columellar recess in the quadrate so as to restrict axial or rotational movement. Although the distal ends of the stapes have not been preserved in other captorhinomorphs, the presence of a deep columellar recess indicates a similar pattern. In ophiacodont and edaphosaurian pelycosaurs, the distal end of the stapes apparently was continued into a shallow columellar recess by a stout stylohyal cartilage.

In both captorhinomorphs and pelycosaurs a stout dorsal process buttressed the mid-dorsal surface of the stapes against the underside of the paroccipital process.

The general appearance of the primitive reptilian stapes was similar to that of the rhipidistian hyomandibula. Like it, the stapes was an important link in the system of cranial kinesis and was not associated with hearing in any way. The fact that the distal end of the rhipidistian hyomandibula abutted the otic capsule predisposed it to be adapted, whenever it became free to vibrate, as a hearing ossicle. The most frequent way in which the hyomandibula was released was through the loss of the primitive neurokinesis and the subsequent freeing of the hyomandibula from its function as part of the kinetic linkage. The hyomandibula was freed different times in several separate lineages. The loss of kinesis in temnospondyl and anthracosaurian labyrinthodont lineages and in several lepospondyl lines led to the development of a number of quite different stapes types.

The transition from a rhipidistian neurokinetic mechanism to a reptilian metakinetic mechanism seems to have occurred almost directly without an intervening labyrinthodont stage and at a relatively small size for either the development of large size and/or akinesis would have released the stapes from its supportive function as happened in the true cotylosaurs.

The reptilian stapes was released a number of times from its function as a braincase support to be incorporated into the middle ear structure. The development of secondary akinesis in pareiasaurs, pelycosaurs, and turtles lead to a change in function by the stapes. The sequence of changes is best illustrated in the pelycosaur-therapsid (synapsid) lineage. The earliest pelycosaurs of which there are good cranial remains indicate that they were already akinetic and that reduction of the stapes had begun. The stapes of *Ophiacodon* was similar to that of captorhinomorphs with only a slight reduction of the proximal end (footplate). In *Dimetrodon*, the stapes, although still quite massive, was further reduced proximally. This reduction, paralleled by the reduction of the quadrate and post-dentary elements of the mandible continued in the therapsid line leading eventually to mammals.

Only two reptilian groups succeeded in freeing the stapes from its function as part of the metakinetic linkage without losing the metakinesis. Both the procolophonids and the diapsids which had a lower metakinetic axis along the paroccipital processes developed large alar processes of the prootics and associated lateral ascending processes of the supraoccipital (Ivakhnenko, 1973). These, in addition to a slender median ascending process of the supraoccipital, contacted the parietal to limit elevation of the skull roof relative to the braincase. The development of alternate limits of skull roof elevation freed the stapes from performing a similar function and permitted it to become reduced and incorporated into the sound conducting apparatus of the middle ear.

CONCLUSIONS

Cranial metakinesis in primitive reptiles functioned as a gape orientation mechanism to synchronize maxillary and mandibular impact on prey items. Typically the mandibular segment contacted the prey item first. Because of the small size of the most primitive reptiles relative to their prey, the mandibular adductor muscles were not capable of accelerating the prey item upward. Instead, the maxillary segment was accelerated downward so that prey was impaled on the caniniform teeth as effectively as if it had been accelerated upward and with less energy expenditure. By synchronizing mandibular and maxillary contact and thus preventing circumferential acceleration of the prey item with its centrifugal force component, the chances of deflecting the prey item from the mouth during prey seizure were greatly diminished.

Loss of cranial metakinesis occurred independently in several lineages. The great weight of the skulls in pareiasaurs and advanced captorhinids prevented any form of elevation of the skull roof by the relatively small constrictor dorsalis musculature thus leading to the akinetic condition found in these groups. The high stresses placed on the occiput by active carnivores apparently led to selection for a more solid occiput to oppose them thus precipitating the loss of kinesis in carnivorous pelycosaurs. The herbivorous edaphosaurian pelycosaurs are believed to have developed from primitive carnivorous or omnivorous pelycosaurs that were already akinetic.

The development of cranial metakinesis presupposes the presence in the amphibian ancestors of reptiles of a dorsally open braincase without a tectum synoticum. Only the true cotylosaurs, a group of amphibians including diadectids, tseajaiids, limnoscelids, and possibly seymouriamorphs (sensu stricto) had such a braincase. The labyrinthodonts including the Anthracosauria (sensu stricto) with which the reptiles have so often been allied have solidly roofed braincases with well developed tecta synotica. All known true cotylosaurs appear too late in the fossil record and are too specialized to have been the ancestors of reptiles. Nevertheless, the similarities between the braincases, humeri, and vertebral columns of the true cotylosaurs and reptiles suggest that they had a common amphibian ancestor.

Metakinetic action requires the presence of a segmented mandibular adductor mass originating from both the skull roof (maxillary segment) and the braincase (occipital segment). The primitively large post-temporal fenestrae remained large in metakinetic reptiles to accommodate swelling of some of these muscles, in particular the M. adductor mandibulae externus profundus. Any tetrapod exhibiting large post-temporal fenestrae is believed to have passed through an evolutionary stage when it was metakinetic. At present, only reptiles are known to have passed through this stage. Where secondary akinesis developed because of increased size, the post-temporal fenestrae remained large. In cases where akinesis evolved in small, active carnivorous forms, reduction of the adductor musculature and a consequent expansion of the occipital plate occurred, causing the post-temporal fenestrae to become reduced.

It is possible to use these observations to establish criteria for differentiating conventional or saurian reptiles ("sauropsids" of Goodrich, 1916; Watson, 1954) from synapsid or mammal-like ("theropsid") reptiles (Fig. 12). Saurian reptiles are distinguished by vertical occiputs with narrow supraoccipitals and paroccipital processes with large post-temporal fenestrae. Metakinesis has been retained by many of the smaller members of the group. Synapsid reptiles are identified by the presence of anterodorsally sloped occiputs with broad supraoccipitals and paroccipital processes with small post-temporal fenestrae. None of these animals is known to have been metakinetic. As a result of these criteria it is possible to identify both procolophonids and pareiasaurs as true saurian reptiles, albeit very primitive members of that group. Likewise captorhinomorphs, perhaps the most generalized group of primitive reptiles related to modern forms, are true saurian reptiles ("sauropsids") not "theropsids" as Watson (1954) thought. Similarly it may be determined that the true cotylosaurs with vertical plate-like occiputs with small post-temporal fenestrae are not true reptiles.

The presence of a dorsal metakinetic axis in primitive reptiles could function only with the presence of a structure that limited excessive elevation of the skull roof. The stapes with solid articulations on both the braincase (cup-shaped foramen magnum) and the quadrate appears to have served this function. Only when akinesis developed (in pelycosaurs, procolophonids, true cotylosaurs) or alternative limiting structures evolved (procolophonids, diapsids) was the stapes freed from its supportive function and adapted as a hearing element.

Osteological characters indicative of cranial metakinesis are believed to have been present in the earliest reptiles laying amniotic eggs since small size was a prerequisite for the development of both metakinesis and the amniotic egg.

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ABBREVIATIONS

Bones of the Skull and Braincase

bo - basioccipital

bsph - basisphenoid

eo - exoccipital

f - frontal

op - opisthotic

pa - parietal

pof - postfrontal

pop - paroccipital process

pp - postparietal

pro - prootic

psph - parasphenoid

pt - pterygoid

q - quadrate

so - supraoccipital

v - vomer

Cranial Arterial System

AAI - Arteria alveolaris inferior

AAS - Arteria alveolaris superior

ACB - Arteria cerebralis

AFR - Arteria frontalis

AIC - Arteria intermandibularis caudalis

AIM - Arteria intermandibularis medialis

AIO - Arteria intermandibularis oralis

AME - Arteria mandibularis externa

AMI - Arteria mandibularis interna

AMN - Arteria mandibularis

AMX - Arteria maxillaris

ANA - Arteria nasalis anterior

ANI - Arteria nasalis inferior

ANL - Arteria nasalis lateralis

AOA - Arteria orbitalis anterior

AOI - Arteria orbitalis inferior

AOS - Arteria orbitalis superior

APA - Arteria palatina anterior

API - Arteria palatina inferior

APL - Arteria palatina lateralis

APM - Arteria palatina medialis

APN - Arteria postnasalis

ASN - Arteria subnasalis

AST - Arteria stapedialis

ATM - Arteria temporalis

ATP - Arteria temporoparietalis

CE - Carotis externa

CI - Carotis interna

Cranial Venous System

SCM - Sinus cerebralis medius

SNA - Sinus nasalis

SOR - Sinus orbitalis

SPL - Sinus palatinus lateralis

SPM - Sinus palatinus medialis

SPT - Sinus palatinus transversalis

VAN - Vena anastomotica

VCL - Vena capitis lateralis

VCL$_p$ - Vena capitis lateralis prima

VCL$_s$ - Vena capitis lateralis secunda

VCM - Vena cerebralis media

VCP - Vena cerebralis posterior

VFR - Vena frontalis

VHL - Vena hypophysialis lateralis

VJC - Vena jugularis communis

VMD - Vena mandibularis

VME - Vena mandibularis externa

VMI$_d$ - Vena mandibularis interna dorsalis

VMI$_v$ - Vena mandibularis interna ventralis

VON - Vena orbitalis

VPF - Vena praefrontalis

VPI - Vena palpebralis inferior

VST - Vena supratemporalis

VTA - Vena tympanica anterior

Cranial Nervous System

II - Optic Nerve

III - Oculomotor Nerve

IV - Trochlear Nerve

V - Trigeminal Nerve

V$_1$ - Ophthalmic ramus of Trigeminal Nerve

V$_2$ - Maxillary ramus of Trigeminal Nerve

V$_3$ - Mandibular ramus of Trigeminal Nerve

V_4 - M. constrictor (I) dorsalis ramus of Trigeminal Nerve
VII - Facial Nerve
VII_{cht} - Chorda tympani ramus of Facial Nerve
VII_{hy} - Hyomandibular ramus of Facial Nerve
VII_p - Palatine ramus of Facial Nerve
VII_{pal} - Lateral palatine ramus of Facial Nerve
IX - Glossopharyngeal Nerve
X - Vagus Nerve
XI - Vagus accessory Nerve
XII - Hypoglossal Nerve

Cranial Musculature

Trigeminally innervated muscles
MAMEM - M. adductor mandibulae externus medius
MAMEP - M. adductor mandibulae externus profundus
MAMES - M. adductor mandibulae externus superficialis
MAMP - M. adductor mandibulae posterior
MCID - M. constrictor (I) dorsalis
MIMD - M. intramandibularis
MLAO - M. levator anguli oris
MLB - M. levator bulbi
MLPT - M. levator pterygoidei
MPPT - M. protractor pterygoidei
MPSTP - M. pseudotemporalis profunda
MPSTS - M. pseudotemporalis superficialis
MPTP - M. pterygoideus profundus
MPTS - M. pterygoideus superficialis
MRAO - M. retractor anguli oris

Intermandibular and Hyoid Musculature

MBMD - M. branchiomandibularis dorsalis

MBMV - M. branchiomandibularis ventralis

MCH - M. coracohyoideus

MGG - M. genioglossus

MGH - M. geniohyoideus

MIMC - M. intermandibularis caudalis

MIMO - M. intermandibularis oralis

MOH - M. omohyoideus

Cervical and Other Musculature

MBUR - M. bursalis

MCM - M. cervicomandibularis

MESCM - M. episternocleidomastoideus

MIARd - M. infra-articularis dorsalis

MICC - M. iliocostalis capitis

MICE - M. intercostalis externa

MICI - M. intercostalis interna

MICIv - M. intercostalis ventralis

MISPce - M. interspinalis cervicus

MLCap - M. latissimus capitis auriculoparietalis

MLCca - M. latissimus capitis transversalis capitis

MLCce - M. latissimus capitis transversalis cervicus

MOCM - M. obliquus capitis magnus

MRCA - M. rectus capitis anterior

MRCP - M. rectus capitis posterior

MTZ - M. trapezius

MSC - M. sphincter colli

MSCa - M. spinalis capitis

Other structures

CB I - Ceratobranchial I

CB II - Ceratobranchial II

EH - Epihyal

Lig. N. - Ligamentum nuchae

LRP - Lateral rictal plate

MC - Metkelian cartilage

MRP - Median rictal plate

PL - Processus lingualis

TM - Tympanic membrane