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THE LOWER JAW OF CYNODONTS (REPTILIA, THERAPSIDA) AND THE EVOLUTIONARY ORIGIN OF MAMMAL-LIKE ADDUCTOR JAW MUSCULATURE

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Abstract

The evolution of the feeding apparatus is described from *Dimetrodon* (a primitive mammal-like reptile representing a pre-therapsid stage of evolution) through theriodont therapsids (moderately and fully advanced carnivorous mammal-like reptiles from which mammals were ultimately derived). Osteological changes are analyzed in terms of modifications in the adductor jaw musculature. In *Dimetrodon,* very primitive theriodonts, and therocephalians, adductor jaw musculature did not descend beneath the zygomatic arch to insert over the lateral surface of the lower jaw. With the exception of M. pterygoideus, the jaw musculature in these animals was confined within the temporal fossa where part of this muscle mass approached the arrangement of M. adductor mandibulae externus (filling the temporal fossa lateral to the mandibular branch of the trigeminus nerve) in living

reptiles. The insertion of this external adductor was probably characterized by a concentrated tendinous attachment to the coronoid eminence or abbreviated coronoid process and a broad fleshy attachment to the dorsal and dorsomedial surfaces of the jaw. In addition there was no origin of adductor jaw musculature from the medial surface of most of the zygomatic arch. Two groups of theriodont therapsids present evidence that each independently departed from the more primitive arrangement of jaw musculature. In gorgonopsians adductor musculature may have descended beneath the zygomatic arch to insert on the lateral surface of the angular. In cynodonts, on the other hand, two major changes occurred. The first change was the appearance of a masseter muscle whose development was intimately related to the postero-ventral expansion of the dentary including the formation of an angular process. The descent of the insertion of this muscle onto the exposed lateral surface of the dentary was accompanied by the establishment of the entire length of the zygomatic arch as an area of muscular origin. The second change was the development of a pattern of insertion characteristic of the mammalian tem-poralis muscle, accomplished through the posterodorsal expansion of the coronoid process of the dentary. The result of these modi-fications was that cynodonts established an arrangement of adductor jaw musculature closely approaching that in living mammals. For this and other reasons cynodonts appear to be excellent candidates for the ancestors of all mammals.

INTRODUCTION

Among known therapsid reptiles, cynodonts show progressive osteological changes in the lower jaw not found in any other group of reptiles. As described in detail by Crompton (1963), cynodonts ranked in a stratigraphic series demonstrate progres-sive enlargement of the posterior part of the dentary and, con-comitantly, reorientation in position and reduction in size of the accessory jaw bones. The enlargement of the dentary involved posterodorsal expansion into a broad, well-developed coronoid process and posteroventral expansion into a well-formed angular region, including in some cases a distinct posteriorly projecting angular process. The magnitude of the total transformation beyond the primitive therapsid condition is great; the result is

the formation, in advanced cynodonts, of a broad mammal-like ramus of the dentary which dominates the posterior one-half of the jaw (the term *ramus* is used here as in human anatomy to distinguish the muscle-bearing *ramus* from the tooth-bearing *body* of the mandible).

Since the changes in this series profoundly altered the entire posterior part of the jaw, it is certain that they were related to modifications of the jaw musculature. Several authors have attempted to define the nature of this relationship. Both Watson (1912) and Parrington (1955) attributed the development of the angle of the dentary to the transfer of the insertion of adductor jaw musculature from the accessory jaw bones. Watson suggested that pterygoideus musculature established an insertion on the medial surface of the angle. Parrington proposed that an insertion of masseteric musculature was transferred from the reflected lamina of the angular to the lateral surface of the angle when the former was reduced and the latter first appeared. A divergent opinion was presented by Patterson and Olson (1961), who suggested that the enlargement of the posteroventral corner of the dentary into an angular process reflected a transition from the reptilian to the mammalian type of depressor musculature.

Crompton (1963) attempted a more extensive analysis in which he reconstructed adductor jaw musculature in advanced cynodonts with a pattern of differentiation and distribution approaching that in living therian mammals. By working back through the cynodont sequence, he proposed greater involvement of the individual mammalian muscle components with the accessory jaw bones correlated with their greater development and the diminished size of the dentary. He reconstructed the temporalis musculature, however, as attaching exclusively to the coronoid process of the dentary in all cynodonts. In non-cynodont theriodonts the complete insertions of all muscles, except the temporalis muscle, were considered to have been on the accessory jaw bones. As a result, Crompton interpreted the modification of the cynodont jaw as reflecting the simple shift onto the dentary of the insertions of four out of the five components of the adductor jaw musculature in therian mammals. Crompton accepted the proposal of Watson and of Parrington that the attachments of portions of the adductor jaw musculature were transferred onto the cynodont angle; he

followed their suggestions exactly except that the pterygoideus muscle of Watson was designated as the internal pterygoid muscle and the masseter muscle of Parrington as the superficial masseter muscle. In addition he suggested the transfer of the insertions of external pterygoid and deep masseter musculature from the accessory jaw bones onto the dentary.

This paper is the initial report of a comprehensive reconstruction of adductor jaw musculature in *Dimetrodon,* which represents a pretherapsid stage of evolution, and in theriodont therapsids. During this study it became apparent that a reinterpretation of the development of the cynodont lower jaw in relation to modifications of certain portions of the adductor jaw musculature was necessary. There are two major reasons why a reinterpretation is indicated. First, evidence in *Dimetrodon* and primitive theriodont therapsids indicates that the reconstruction of musculature occupying the temporal fossa in these forms can validly be based on the details of the distribution of M. adductor mandibulae externus in living reptiles. The consideration of this reptilian arrangement as antecedent to cynodonts provides a new assessment of the type and magnitude of the muscular changes reflected in the development of the cynodont jaw. Second, examination of *Dimetrodon* and theriodont therapsids indicates that a masseter-like muscle was not present in the ancestors of cynodonts. Parrington's generalization (1955, pp. 24-27; also see Cox, 1959; Ewer, 1961; and Crompton, 1963, all of whom accepted this generalization) that the reflected lamina of the synapsid angular served for the insertion of a masseter muscle is rejected and, consequently, so are Parrington's and Crompton's hypotheses that masseteric musculature was gradually transferred from the reflected lamina to the dentary during cynodont evolution. It is concluded here that cynodonts developed a masseter-like muscle but that they did so in a manner different from that proposed by either of these authors.

Finally, this study has raised problems concerning phylogenetic relationships. The morphological changes undergone by the cynodont lower jaw and the possible muscular transformations reflected therein suggest a need for re-evaluation of phylogenetic relationships among advanced therapsids and early mammals, specifically the suggestions that some or all mammals were derived from

bauriamorphs (see Romer, 1961) and that the ictidosaur *Diarthrognathus* was derived from scaloposaurids (Crompton, 1958).

MATERIALS

Adductor jaw musculature was dissected specifically for this report in the following: *Alligator, Iguana, Chelonia, Terrapene* and *Sphenodon* (partial) among reptiles, and *Didelphis, Solenodon, Erinaceus, Canis, Sylvilagus, Macacus* and *Homo* among mammals. In addition many of the observations on the modern patterns of muscle differentiation and distribution, as well as on the relationship of bone structure to muscle attachment, have been based on dissections made in the past over a much wider range of reptiles and mammals. Extensive collections of captorhinomorph, pelycosaur, and therapsid fossil material forming the subject of this study were gathered from the various sources cited in the acknowledgments. The following is a list of abbreviations of institutions whose specimens are cited in this paper.

AMNH	American Museum of Natural History, New York, N.Y.
FMNH	Field Museum of Natural History, Chicago, Ill.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
PIN	Paleontological Institute, Moscow, U.S.S.R.
SAM	South African Museum, Capetown, South Africa
UC	University of California, Berkeley, Calif.
YPM	Peabody Museum, Yale University, New Haven, Conn.

KEY TO TEXT — FIGURE ABBREVIATIONS

An	Angular
An C	Angular Crest
Ant F	Anterior Fossa
Ant P	Anterior Process
Apon	Aponeurosis presumed to cover the lateral temporal fenestra in *Dimetrodon*
BO	Bodenaponeurosis
C1, C2, C3?	Concavities on the Lateral Surface of the Reflected Lamina of *Bauria*
Conn Rf Lam-An Body	Connection between the Body and Reflected Lamina of the Angular
Dent	Dentary
Dent (CP)	Coronoid Process of the Dentary
Dev M Mass	Developing Masseteric Musculature

Int Pt Vac	Interpterygoidal Vacuity
Ju	Jugal
Med Pt Crest	Medial Pterygoid Crest
MAME	Adductor Mandibulae Externus Muscle
MAMIP[s]	Adductor Mandibulae Internus Pseudotemporalis Muscle
MAMIP[t]	Adductor Mandibulae Internus Pterygoideus Muscle
M Add Post	Adductor Mandibulae Posterior Muscle
M Mass Pr	Deep Part of the Masseter Muscle
M Mass Supf	Superficial Part of the Masseter Muscle
M Pt Ex	External Pterygoid Muscle
M Pt Int	Internal Pterygoid Muscle
M Temp Pr	Deep Part of the Temporalis Muscle
M Temp Supf	Superficial Part of the Temporalis Muscle
M Zygo-mand	Zygomaticomandibularis Muscle
Pa	Prearticular
Post F	Posterior Fossa
Quad R Pt	Quadrate Ramus of the Pterygoid
R1, R2, R3	Ridges on the Lateral Surface of the Reflected Lamina of *Bauria*
Retr Pr	Retroarticular Process
Rf Lam	Reflected Lamina
Sa	Surangular
Sag C	Sagittal Crest
Stria	Striations
Temp Apon	Temporal Aponeurosis
Temp F	Temporal Fossa
Tend M Mass Supf	Tendon of the Superficial Masseter Muscle
Trans Pr Pt	Transverse Process of the Pterygoid
VR	Vertical (Main) Ridge of the Angular
Zyg Arch	Zygomatic Arch

The Distribution of External Adductor Jaw Musculature[1] in *DIMETRODON*

Parrington (1955, p. 25, fig. 12B) postulated that adductor jaw musculature emerged from the temporal fossa and established an insertion on the exposed lateral surface of the jaw at a pre-pelycosaurian stage of evolution. According to his hypothesis, it inserted on the lateral surface of the keeled angular in primitive pelycosaurs and the insertional area was retained on the anterior

[1] Musculature positioned lateral to the mandibular division of the trigeminal nerve. This position is occupied by the adductor mandibulae externus muscle in reptiles and the masseter, temporalis, and external pterygoid muscles in mammals.

segment of this keel left as the reflected lamina of the angular in sphenacodonts and therapsids. In pelycosaurs and therapsids this musculature was reconstructed as taking origin from the ventral surface of the anterior root of the zygomatic arch. Therefore, if Parrington's hypothesis is correct, all synapsids possessed a muscle mass closely approaching the topography of the superficial component of the mammalian masseter muscle.

During the course of this study, it became apparent that there is little, if any, evidence to support Parrington's hypothesis. In fact, a body of evidence which tends to controvert it has been gathered from multiple sources among synapsids. Important to my conclusion that masseteric musculature was not differentiated in prepelycosaurs and was not present throughout synapsids is the structure of the lateral surface of the angular in one specimen of *Dimetrodon milleri* (MCZ 1361), the only example of this genus studied giving evidence to relate this surface to soft structure of any kind. Channels are found over the entire lateral surface of the left angular. Channeling is also present on the anterior two-thirds of the right angular (pl. 1) where it is very well-developed and heavy. Presumably, in life, it was also present on the posterior one-third of the lamina, but the surface is not well enough preserved to make this certain.

In other specimens representing this general level of evolutionary development, similar channeling can be found on highly probable dermis-bearing surfaces. It is found on the outer surface of the dentaries of *D. limbatus* (FMNH UC 1001) and the brithopodid *Syodon* (PIN 157/77; Olson, 1962, pl. 13F), and covers the snout of the phthinosuchid *Eotitanosuchus* (PIN 1580/1; Olson, 1962, pl. 12A). The position of this channeling suggests dermal vascular and nerve supply coursing about on the surface of the bone immediately under appressed skin as occurs in some modern turtles. Channels are variably developed on the dermis-bearing surface of the skull of *Chelonia mydas* and are sometimes well-developed on the skull of the pleurodire turtle, *Podocnemis*. In *Chelonia,* studied by thin sections, these channels carry nerves and blood vessels to the closely applied dermis. The association of channels with dermis-bearing surfaces, therefore, suggests that skin, not musculature, attached to the lateral surface of the angular, including the reflected lamina of *Dimetrodon*.

In other pelycosaurs studied there is no direct evidence of the attachment of skin to the lateral surface of the posterior part of the jaw. However, there are other anatomical features of pelycosaurs and also of captorhinomorphs which support the contention, suggested by the evidence in *Dimetrodon,* that a masseter-like muscle was not differentiated at a prepelycosaurian stage of evolution.

In well-preserved specimens of *Captorhinus* typical dermal pitting covers the posterolateral part of the jaw and indicates that adductor jaw musculature was not exposed ventral to the level of the cheek but was instead confined within the temporal fossa. In addition, as is seen in Text-figure 1, *Captorhinus* shows that there was very little space available for the potential emergence of musculature out from under the cheek. The convex lateral surface of the adducted jaw comes very close to the entire ventral edge of the cheek.

No captorhinomorph or pelycosaur examined shows evidence of the attachment of adductor jaw musculature to any part of the exposed lateral surface of the jaw. As far as can be determined the dorsolateral surface of the jaw is convex in *Limnoscelis,* in the
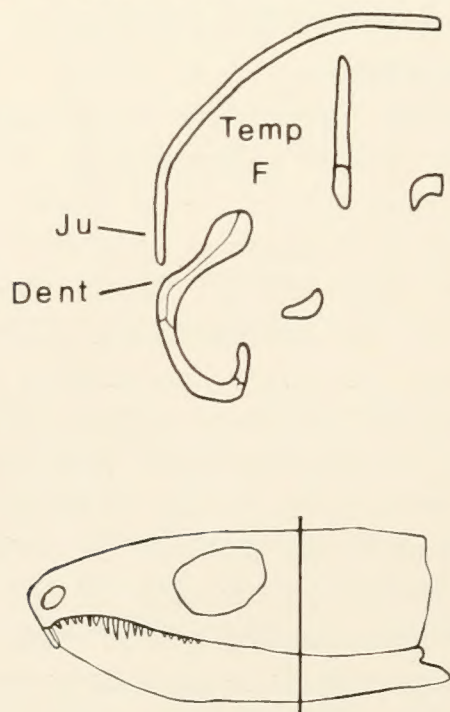
Text-fig. 1. Transverse section through the temporal region in *Captorhinus* illustrating the relationship of the cheek to the adducted lower jaw. (Section based on FMNH UC 242.)

pelycosaur-like *Protorothyris* and in *Eothyris* (pl. 3) representing primitive pelycosaurs; the only morphological departure in this area from *Captorhinus* is the absence of dermal pitting. Since there is no evidence to warrant the reconstruction of musculature, it is easy to regard the absence of such pitting as a consequence of preservation, preparation or the fact that skin commonly attaches to bone without leaving evidence of its presence. There are, as will be reported in a later section, other functions to account for the presence of the keel of the angular in *Protorothyris* and in pelycosaurs.

A close relationship between cheek and jaw is found throughout captorhinomorphs and pelycosaurs. In the skulls of *Limnoscelis* (YPM 811), *Protorothyris* (e.g., MCZ 2147, 2148), *Eothyris* (MCZ 1161), *Ophiacodon* (MCZ 1366), and *Dimetrodon* (many specimens) which were examined, the inferior border of the cheek, as preserved, consistently appears as a direct posterolateral continuation of the upper tooth row and parallels the outer surface of the lower jaw. When upper and lower tooth rows are placed in occlusion it is apparent that the superolateral border of the jaw closely approaches the inferior border of the cheek (pl. 3) as in *Captorhinus*. This also is seemingly true for caseids (see Romer and Price, 1940, pls. 19 and 20) and perhaps for edaphosaurids, although in some specimens of *Edaphosaurus* the zygomatic arch is dorsally displaced away from the lower jaw (see Romer and Price, 1940, fig. 6).

Assuming that no musculature was exposed in the ancestors of captorhinomorphs and hence pelycosaurs (this is simpler, I believe, than to assume *Captorhinus* lost exposed musculature hypothetically present in its ancestry) there is no indication in the specimens studied, except the specialized *Edaphosaurus,* that a channel was ever formed between the skull and jaw to suggest the possibility that musculature had invaded the exposed lateral surface of the jaw. Any slight gaps present between the jaw and cheek would be expected to have housed a skin fold, as in modern reptiles, necessary to provide slack in the skin for opening the jaw. It is clear that none of these animals present evidence that they were in a transitional stage leading to the establishment of a masseter-like muscle or that they had ancestors that ever went through such a stage.

If, then, no musculature attached to the exposed portion of the jaw in *Dimetrodon*, the question remains as to how the musculature was organized within the temporal fossa. Watson (1948, figs. 4 and 5) and Fox (1964, fig. 5) have attempted this reconstruction of *Dimetrodon* in some detail. However, my study of the morphology of the skull and jaws of *Dimetrodon* and of modern reptiles as models for reconstruction points to another and, I believe, more appropriate concept of the arrangement of adductor jaw musculature.

In *Dimetrodon incisivus* (AMNH 4636) a rugose surface is found on the posterior tip of the dentary at the dorsal summit of the coronoid eminence. A keel, forming the anterior two-thirds of the dorsal edge of the surangular, runs posteriorly from the rugose area. The rugosity strongly suggests a tendinous attachment and the keel suggests that this attachment may have extended posteriorly as a thin aponeurotic sheet. This evidence of tendinous attachment plus the general reptilian structure of the lower jaw and temporal region in *Dimetrodon* is consistent with the reconstruction of a type of muscle distribution that is found in many living reptiles. Modern reptiles possessing a coronoid eminence or process raised above the level of the jaw articulation (turtles, *Sphenodon*, and lizards) invariably have a tendon ("bodenaponeurosis", Lakjer, 1926) attached to this structure (Attach Bo, text-fig. 3C). A "bodenaponeurosis" similar in its relationships to that in the modern forms is reconstructed for *Dimetrodon*, attaching to the coronoid eminence and the keeled dorsal surface of the surangular, in Text-figure 2. In living reptiles the broad lateral and medial surfaces of this tendon serve for the insertion of the majority of M. adductor mandibulae externus muscle fibers which occupy the entire lateral portion of the temporal fossa dorsolateral to the mandibular and maxillary divisions of the trigeminal nerve. Again on the basis of a modern reptilian model, musculature with a similar insertion (arrows, text-fig. 2) in *Dimetrodon* would be expected to have an origin in the far reaches of the temporal fossa, including the ventral surface of the temporal roof, the medial surface of the dorsolateral portion of the cheek and much of the anterior surface of the posterior wall of the fossa. In addition to a tendon, the insertion of the adductor mandibulae externus musculature in *Dimetrodon* would also be

expected to have included a fleshy attachment to the dorsomedial, dorsolateral and posterodorsal surfaces of the lower jaw.

The ventral limit of the insertion to the dorsomedial surface of the surangular reconstructed in Text-figure 3A is based directly on the arrangement in *Iguana* (text-fig. 3C) where this portion of the surangular is set off from the lateral wall of the Meckelian fossa in precisely the same manner as in *Dimetrodon*. When an aponeurosis (BO text-fig. 3C) attaches to the coronoid region in
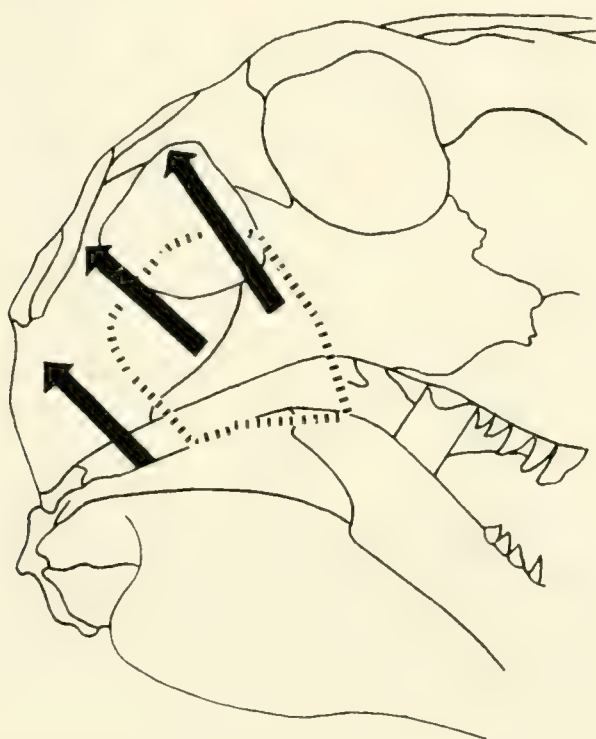
Text-fig. 2. Lateral view of the posterior part of the skull and jaw of *Dimetrodon*. The dashed line represents the outline of the "bodenaponeurosis" reconstructed from a modern reptilian model. Reconstruction of adductor mandibulae externus musculature is represented by arrows. (Outline after Romer and Price.)

modern reptiles, the musculature arising from the undersurface of the temporal roof (lateral to the sagittal plane of the epipterygoid) and cheek inserts only on the dorsal portions of the jaw and, for the most part, to the aponeurosis; it does not extend ventrally to insert into the Meckelian fossa. In large part this is the area of insertion of M. adductor posterior, Text-figure 3C, arising from the medial portion of the quadrate. Thus there is no
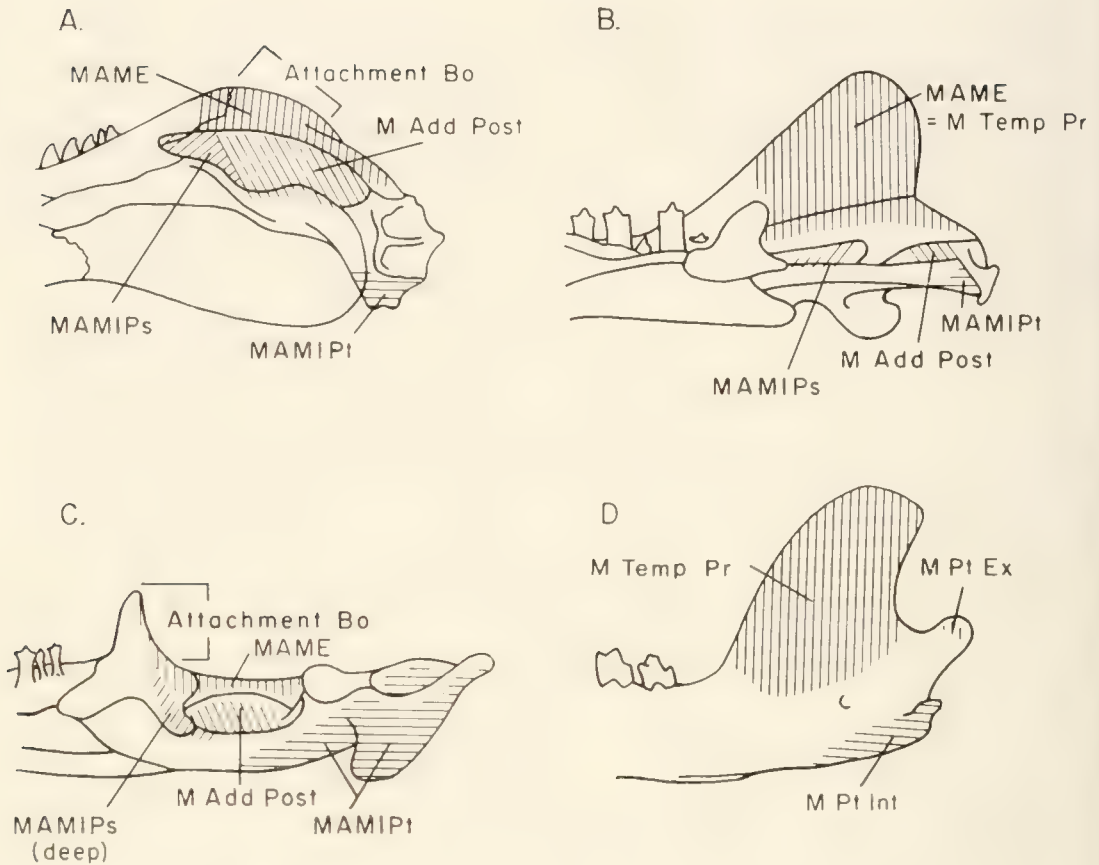
Text-fig. 3. Medial views of the lower jaws of: A. *Dimetrodon*, B. *Thrinaxodon*, C. *Iguana*, D. *Didelphis*. The reconstruction of the insertion of adductor jaw musculature in *Dimetrodon* is based on the arrangement in *Iguana*; that in *Thrinaxodon* is based on both *Iguana* and *Didelphis*. (Jaw outline in A after Romer and Price; in B after Crompton.)

modern analogue for the reconstructions made by Watson (1948) and Fox (1964) depicting "temporalis" musculature arising from the undersurface of the temporal roof and (according to Fox) the dorsal portion of the cheek and inserting into the Meckelian fossa. In Text-figure 3A the insertions of adductor posterior and pseudotemporalis musculature are reconstructed within the confines of the Meckelian fossa.

Direct evidence of muscle attachment to the dorsolateral surface of the jaw, similar to the depression on the posterior tip of the dentary described for *Dimetrodon* by Watson (1948), has not been found in any jaw examined. However, if present, the insertion in this area probably was very minor. Under the conditions described for *Dimetrodon* the ventral extent of muscular insertion

to the lateral surface of the jaw would have been limited by the close proximity of the zygomatic arch to the closed jaw and by the attachment of skin to the exposed lateral surface of the jaw. Finally, muscle fibers (posterior arrow, text-fig. 2) arising from the ventrolateral portion of the posterior wall of the temporal fossa would be expected to have inserted fleshily on the rounded dorsal surface of the posterior part of the surangular in *Dimetrodon*.

Assuming the character of muscular insertion reconstructed above, it does not appear reasonable to expect that any part of the zygomatic arch, except the posterior-most portion of its medial surface, served as an area of origin for adductor jaw musculature. Muscle fibers arising from the medial surface of the zygomatic arch, as Fox (1964) suggested for a "masseter" muscle, would have had to insert on the dorsolateral edge of the jaw or the lateral surface of the "bodenaponeurosis". Such an arrangement does not seem to be functionally feasible for the following reasons.

Haines (1934, cited by Parrington, 1955) determined in cadavers that muscle fibers of long action normally stretch by a maximum of 132.6% of their contracted length. Assuming that this figure approaches the maximum stretch of which such fibers are capable, fibers arising from the inner surface of the zygomatic arch in *Dimetrodon* would not be of sufficient length to permit a reasonable gape for a carnivorous animal. Fibers arising on the medial surface of the anterior portions of the arch would have had to be capable of stretching by an amount exceeding 300% of their contracted length to permit a gape of 40° (text-fig. 4). Under experimental conditions muscle fibers, when stretched by an amount approximately 233% of the shortest length at which they are capable of creating tension, will tear their sarcolemma. Stretch by an amount excessively beyond 117% of the shortest length at which tension can be created is irreversible and is greatly resisted by the elastic properties of the muscle fibers themselves (figures derived from Zierler, 1961, p. 983 and fig. 375). The fact that there are definite limits to the extent by which a muscle can be stretched and that they are of the order of magnitude stated, indicates that the stretch required for musculature to have taken origin from the anterior part of the zygomatic arch in *Dimetrodon* far exceeds the capability of vertebrate muscle. It also suggests that the figure given by Haines probably approaches

a maximum, even allowing for a generous amount of variation in fibers of different muscles.

These functional limitations indicate that modern reptiles alone are appropriate models for the reconstruction of muscular attachment to the lateral wall of the temporal fossa. In Text-figure 4 muscle fibers taking origin from the lateral wall of the temporal fossa posterodorsal to the "132.6% line" and inserting near the dorsal edge of the jaw would have stretched by the amount of 132.6% or less of their contracted length (measured with jaws closed) to open the jaw 40°. Thus they would have been of suf-

132.6%
Line

40°
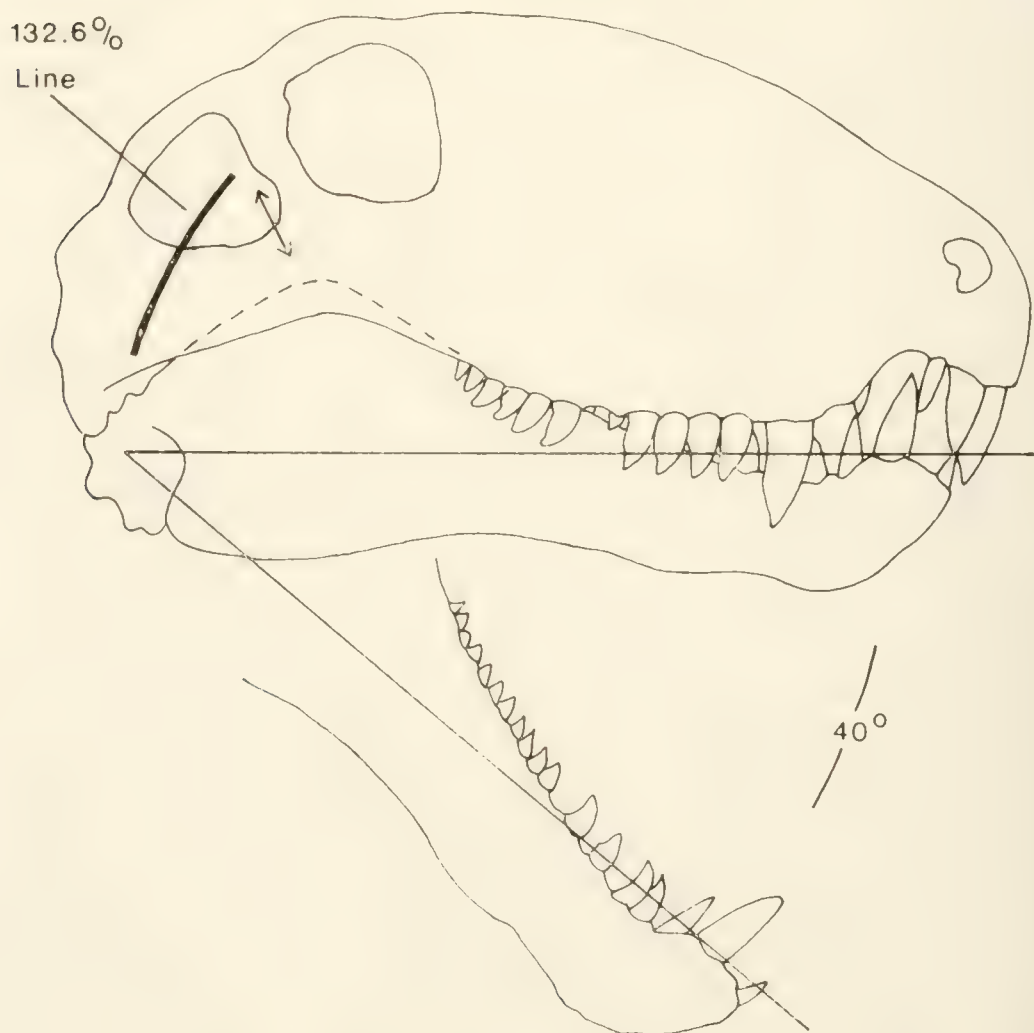
Text-fig. 4.   Lateral view of the skull and jaw of *Dimetrodon* to illustrate the anteroventral limit of muscular attachment to the inner surface of the cheek. The following are assumed: a gape of 40°, muscle fiber direction as indicated by the arrow, and maximum muscle stretch as indicated in the text. (Skull and jaw outlines after Romer and Price.)

ficient length when shortened to allow a reasonable gape for a carnivorous animal. The possible area of origin thus outlined closely approximates the actual origin of the adductor mandibulae externus musculature on the cheek or its remnants in living reptiles. The inferior-most portions of the cheek in living reptiles, including the lower temporal bar in diapsids, do not serve for the origin of adductor jaw musculature. Acceptance of the 132.6% line in Text-figure 4 as the ventral limit of potential muscle origin, plus the indication that skin was attached to the exposed lateral surface of the jaw, leads directly to the conclusion that there was no musculature whatsoever in *Dimetrodon* approaching the relationships of a mammalian masseter muscle. Such musculature was yet to be differentiated from an external adductor muscle mass, the reconstruction of which must be based on a reptilian pattern.

The Distribution of External Adductor Jaw Musculature in Non-Cynodont Theriodont Therapsids

At all levels of evolutionary development, non-cynodont theriodonts show varying degrees of modification in the form of the temporal roof and or posterior wall of the temporal fossa. Those portions of the walls of the temporal fossa on which the origin of adductor mandibulae externus musculature has been reconstructed in *Dimetrodon* were gradually altered during theriodont evolution to a form closely paralleling the area of origin of the temporalis muscle in modern mammals. With the exception of gorgonopsians, however, there appears to have been little change beyond the condition in *Dimetrodon* in the general pattern of *insertion* of external adductor musculature or in the relationship of jaw musculature to the zygomatic arch. This conclusion is based on detailed examinations of the skulls of the brithopodid *Syodon* and the bauriamorph *Bauria*. Gorgonopsians, on the other hand, appear to constitute a special case with respect to the organization of adductor jaw musculature as inferred from the angular of an unidentified form.

SYODON

A specimen of the brithopodid *Syodon* (PIN 157 2) representing a primitive level of theriodont development was studied

from the original photographs published by Olson (1962, pl. 13C, D, E, F, G). Observations relating to the lateral surface of the jaw were confirmed by Dr. L. P. Tatarinov of the Paleontological Museum, Moscow.

The structure of the lateral surface of the jaw in *Syodon* supports the conclusion that adductor musculature was not exposed beneath the zygomatic arch. The entire lateral surface of the reflected lamina is roughened in a manner which, according to Tatarinov, is not significantly different from other parts of the skull, such as the snout, that are difficult to regard as anything but dermis-bearing surfaces. Tatarinov has also informed me that in another primitive theriodont, *Phthinosuchus,* the reflected lamina is slightly roughened and that this also may be true for *Biarmosuchus.* The surface of the reflected lamina in *Syodon* contrasts with the smooth surfaces of muscle-bearing areas in the same specimen (i.e., the walls of the temporal fossa). At face value this evidence suggests the attachment of dermis over most of the lateral surface of the posterior part of the jaw, except that portion of the main body of the angular found medial and posterior to the reflected lamina. The latter surface probably served for the insertion of pterygoideus musculature (see Watson's, 1948, conclusions for *Dimetrodon*). Since the evidence in *Syodon* suggests that the insertion of external adductor musculature would have been restricted to a dorsal position, origin of muscle fibers from the greater part of the zygomatic arch would also be precluded on functional grounds as in *Dimetrodon.* Support for this opinion emerges from the fact that the lateral surface of the coronoid eminence lies medial to, and in close proximity with, the zygomatic arch when the jaw is adducted (determination based on Orlov, 1958, fig. 7 and Olson, 1962, pl. 13D). It appears that physical access of muscle fibers to the entire medial surface of the anterior one-half of the zygomatic arch would have been blocked by this relationship. Finally, from analogy with modern reptiles, a "bodenaponeurosis" would be expected to have attached to the prominent coronoid eminence formed by the dentary and surangular.

BAURIA

The structure of the angular, including the reflected lamina, (text-fig. 5A and pl. 4) in the specimen of *Bauria* (AMNH 5622)

examined is representative of a type found in therocephalians and bauriamorphs in general. It compares closely with the angular and reflected lamina in the scaloposaurid *Ictidosuchops* (Crompton, 1955, fig. 2), the whaitsid *Aneugomphius* (Brink, 1956, fig. 36) and an acid-prepared specimen of a pristerognathid therocephalian, *Ptomalestes avidus* (SAM 11942), studied from stereophotographs. The lateral surface of the angular is markedly modified beyond the primitive condition. The presence of fossae and ridges seems to preclude the interpretation that skin was directly attached. However, inasmuch as the structure of this surface does not meet expectations for the insertion of adductor jaw musculature, therocephalians and bauriamorphs represent an advanced level of theriodont development which has not departed from the condition in *Dimetrodon*, i.e., adductor jaw musculature was not present exposed beneath the zygomatic arch.

In *Bauria* (text-fig. 5A) the lateral surface of the reflected lamina consists of a series of continuous folds. The convexities of these folds are formed by three ridges (R_1-R_3, text-fig. 5A) which radiate outward from a common attachment to a strong curved crest traversing the main body of the angular (An C). In this specimen the area of the convergence of the ridges constitutes the entire attachment of the lamina to the remainder of the jaw. The concavities (C_1-C_2) of the folds, floored by very thin bone, appear as fossae between the 1st and 2nd, and 2nd and 3rd ridges. It is possible that the gap existing anteriorly between the lamina and the angular crest was filled in life by a bony connection and thus formed a third concavity (C_3?, text-fig. 5A). In the scaloposaurid and therocephalians mentioned above, this gap is closed. The width of the fossae increases markedly toward the outer edge of the lamina. Proximally, the fossae have definite boundaries formed by the ridges as they converge and interconnect at their attachment to the main body of the angular. The concavities have no raised margins distally although whether this was the life condition is obscured by the fact that the posterior and ventral edges of the lamina are not complete in this specimen.

The fossae on the lateral surface of the reflected lamina suggest the possibility of muscular attachment; however, they do not suggest the insertion of adductor jaw musculature. In modern vertebrates, fossae are commonly excavated into the lateral sur-

face of the jaw by musculature. In such cases, clearly seen when the muscle mass lies flat against the jaw and inserts at low angle, the defining margin raised from the floor of the fossa is found along the edge of muscular attachment distal to the body of the muscle mass; it is not found on that part of the jaw directly overlain by the muscle. If, in *Bauria,* musculature had descended from the zygomatic arch and inserted on the reflected lamina, the ridged margins of the fossae on this lamina would have been interposed between the areas of insertion and origin. This is not to be expected on the basis of modern analogues. Since the definite margins are found on the proximal part of the lamina, as preserved, and the fossae expand distally, if musculature inserted into these areas, it had to have a ventral or posteroventral source, thereby excluding adductor jaw musculature. The presence of two separate fossae suggests the attachment of at least two separate slips of musculature.

The attachment of ventral musculature (but not necessarily a depressor muscle as suggested by Janensch, 1952) may prove to be the most satisfactory primary and consistent function that can be inferred for the angular keel of primitive pelycosaurs and the reflected lamina of more advanced synapsids. There are suggestions that musculature attached to the ventral part of the lamina in other synapsids as well as in *Bauria.* Indications of striations are found along the ventral edge of the angular in some specimens of *Dimetrodon* and striations are well developed on that part of the ventral edge preserved in the gorgonopsian angular studied (Stria, text-fig. 5B). These are similar to striations sometimes marking the attachment of the temporal aponeurosis to the sagittal and lambdoidal crests in modern mammals. Using modern reptiles as models there are three muscles which might possibly have attached, either singly or in combination, to the lamina. They are the pterygoideus, intermandibularis and branchiomandibularis (variably subdivided) muscles. The latter, which in lizards functions to depress the hyoid apparatus, thereby increasing the size of the oral cavity (Oelrich, 1956), attaches to the ventral edge of the jaw in this general vicinity (see Lubosch, 1933). While all three muscles may have originally attached to the angular keel in primitive pelycosaurs and to the massive reflected lamina in sphenacodonts and early therapsids (pterygoideus on the medial
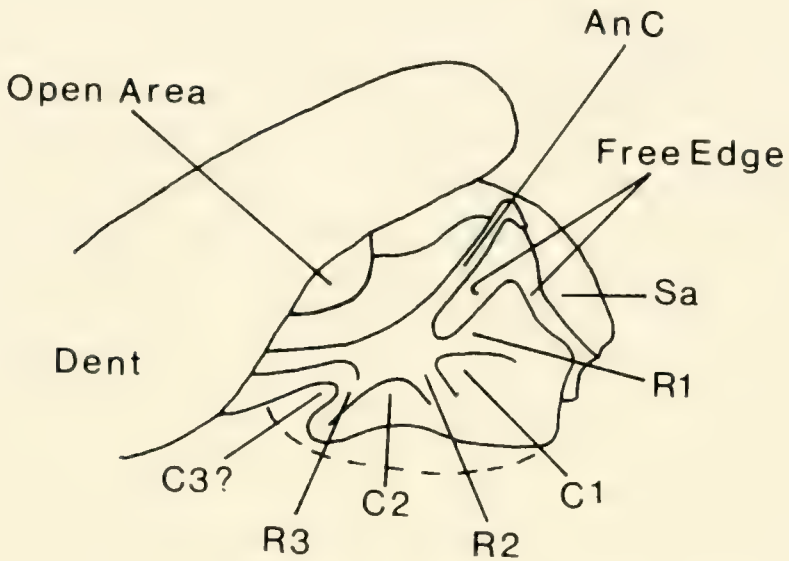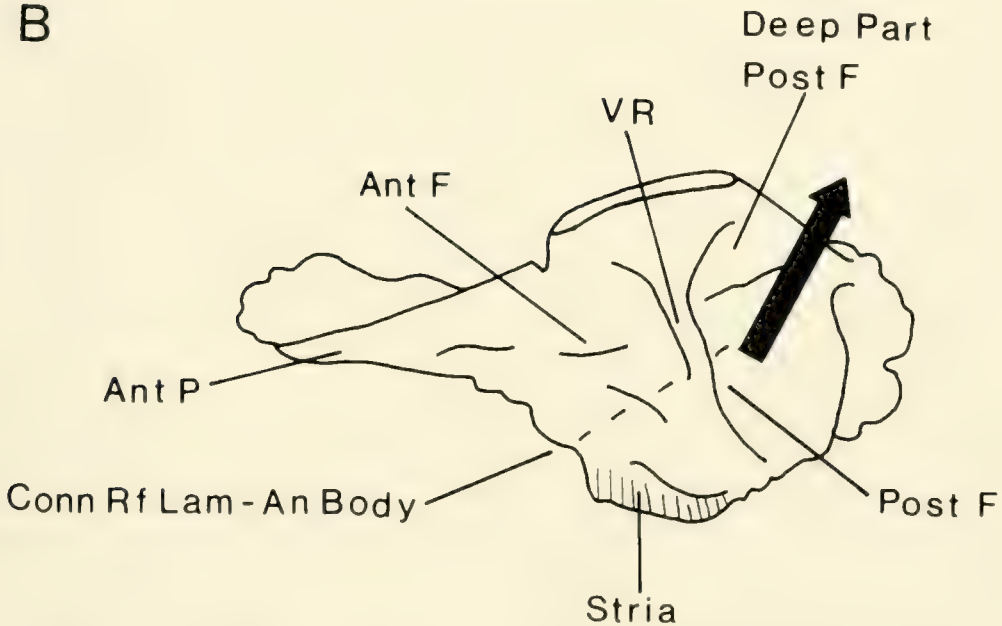
Text-fig. 5. Lateral view of the reflected lamina and body of the angular of: A. *Bauria,* B. an unidentified gorgonopsian. In B the arrow represents a possible arrangement of musculature based on the orientation of the fossa (see text); dashed line (Conn Rf Lam — An Body) represents the approximate level of the connection between the reflected lamina and body of the angular. (B modified slightly from Parrington, 1955.) Not to scale.

surface, intermandibularis and branchiomandibularis on the ventral edge), branchiomandibularis musculature appears to be the best choice to have attached to the reflected lamina in all synapsids. Since it is a relatively small muscle pulling posteriorly, the reflected lamina is adequately supported against such a pull throughout the synapsid series. It is much more difficult to imagine the delicate and reduced lamina of *Bauria* and cynodonts resisting a major medial pull created by pterygoideus musculature. If pterygoideus musculature originally attached to the lamina, this attachment was presumably lost in therocephalians, bauriamorphs and cynodonts. In *Bauria* the posterior fossa (C1, text-fig. 5A) may reflect an attachment of branchiomandibularis musculature established on the lateral surface of the lamina. The anterior fossae (C2 and C3?, text-fig. 5A) conceivably indicate the attachment of slips of a thin sheet of intermandibularis musculature running ventromedially between the jaws external to the belly of the pterygoideus muscle. In cynodonts (pls. 1 and 6), however, the abbreviated size and conspicuous posterior orientation of the lamina suggest that only musculature with a posteroventral line of action attached to this structure (also see p. 25). The reflected lamina in that group may represent a remnant of bone left solely to function for the attachment of branchiomandibularis musculature (the attachment of intermandibularis musculature may have shifted entirely to the enlarged dentary). This provides a functional explanation for the retention of the reflected lamina prior to its becoming the tympanic ring.

The manner in which the reflected lamina is supported in *Bauria* is also difficult to reconcile with the insertion of adductor jaw musculature. This is true for either a muscle mass descending posteroventrally from an origin on the anterior portion of the zygomatic arch, as reconstructed in a pristerognathid therocephalian by Crompton (1963, figs. 13A and B) following Parrington's hypothesis, or a muscle descending downward and slightly anteriorly from an origin on the posterior segment of the zygomatic arch, as is reconstructed in gorgonopsians here (see p. 24). The dorsal margin (Free Edge, text-fig. 5A) of the posterior one-half of the lamina in *Bauria* is free and unsupported. The free border has the effect of leaving approximately one-third of the lamina unsupported at right angles to the direction of muscle pull if an

anterodorsally directed adductor muscle is reconstructed. This does not meet expectations derived from observing the modern mammalian angle where musculature of similar orientation inserts and the angle is supported in the direction of its pull. Other possible reconstructions of adductor jaw musculature would also require atypical support arrangements. Approximately one-half of the reflected lamina would be unsupported if a muscle mass descended downward from the posterior part of the zygomatic arch.

Though extremely difficult to interpret, the morphology of the anterodorsal portion of the angular in *Bauria* does not conform to expectations for the insertion of adductor musculature either. This area is bounded in front by the posterior border of the dentary which is sharply set out from the lateral surface of the angular (see pl. 4). Behind, the area is limited by the curving angular crest. The depressed interval between these two boundaries is fusiform in outline with a conspicuous portion of its floor interrupted by an area entirely free of bone (Open Area, text-fig. 5A). According to Crompton (1955, fig. 2B), most of this interval is also free of bone in the scaloposaurid *Ictidosuchops*. There is, in my mind, no satisfactory explanation to account for the morphology of this depression. Because of its fusiform shape the interval certainly does not appear to have resulted from an excavation of the jaw by the mechanical action of muscular attachment. An area of attachment so outlined and oriented would be atypical, in the extreme, for adductor jaw musculature lying flat against the jaw. Since the attachment of adductor jaw musculature in modern vertebrates is characterized by broad fleshy as well as tendinous attachment, it does not appear reasonable to reconstruct a tendinous attachment to the angular crest without contemplating fleshy attachment to the interval in front of the crest; if the latter is contemplated, it immediately refers back to the problem concerning the outline and orientation of the depression.

Other aspects of the morphology of *Bauria* also indicate, or at least suggest, that much of the pattern of muscular distribution reconstructed for *Dimetrodon* persisted to this advanced level of theriodont development. In *Bauria* specifically, and in therocephalians generally, the modern analogue available for the interpretation of the character of muscular insertion to the abbreviated

but raised coronoid process of the dentary (see text-fig. 5A) is the attachment of the "bodenaponeurosis" in modern reptiles. In *Bauria*, as is seen in transverse section (text-fig. 6), the attachment of musculature was apparently excluded from a substantial amount of the medial surface of the zygomatic arch, because only a minor gap exists between the lateral surface of the coronoid process and the zygomatic arch.
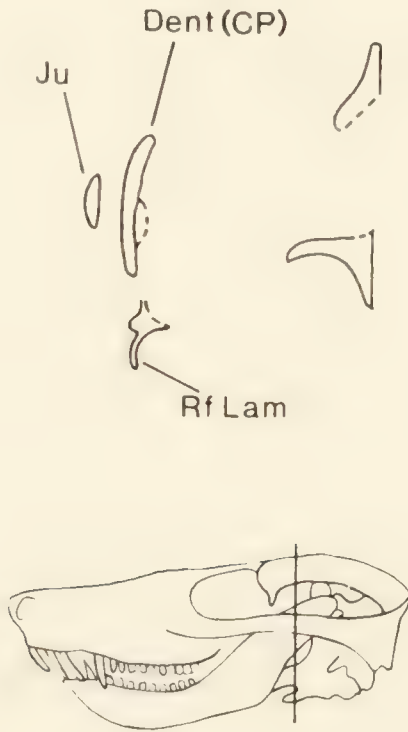
Text-fig. 6.   Transverse section through the temporal region in *Bauria* illustrating the relationship of the zygomatic arch to the coronoid process of the adducted jaw. (Section based on AMNH 5622.)

AN UNIDENTIFIED GORGONOPSIAN

A remarkably well-preserved, isolated left angular of an un-identified gorgonopsian (text-fig. 5B; pl. 5) has been studied. It was originally described and figured by Parrington (1955, p. 5 and fig. 2). He used it in arriving at the conclusion that the reflected lamina in gorgonopsians, and hence presumably in all synapsids, served for the insertion of a masseter muscle descending posteroventrally from an origin on the ventral surface of the anterior root of the zygomatic arch (see Parrington, 1955, p. 24, and fig. 11). The structure of this angular does suggest that

adductor jaw musculature inserted on the exposed lateral surface of the jaw; however, the muscle reconstruction offered here contrasts greatly with the reconstruction made by Parrington.

Two major fossae are present on the lateral surface of this angular, one in front of and the other behind a well-developed vertically oriented ridge (VR, text-fig. 5B) which begins superiorly on the main body of the angular and terminates inferiorly on the reflected lamina. This ridge forms the anterior and, for a short distance, the anterodorsal and anteroventral margins of the posterior fossa (Post F, text-fig. 5B) which is broadly open and lacks a margin posteriorly. Dorsally, this fossa is deeply excavated into the body of the angular, extending well forward beneath the vertical ridge. Below the level of the attachment of the lamina to the body, the fossa becomes much shallower and extends ventrally over the posterior portion of the lamina. In front of the main ridge the more vaguely defined anterior fossa (Ant F, text-fig. 5B) occupies much of the lateral surface of the body of the angular. Its floor is continuous anteriorly with the lateral surface of the anterior projection (Ant P, text-fig. 5B) of the angular which in life underlay and supported the dentary. The moderately sloping anterior surface of the main ridge (VR, text-fig. 5B) of the angular forms the posterior margin of this fossa. The sloping surface of the body of the angular, as it flares laterally onto the reflected lamina, forms the posteroventral margin. Judging from this specimen, the development of the anterior fossa appears to have resulted from the combined presence of the vertical ridge plus the ventrolateral flare of the angular as it forms the reflected lamina. Since the vertical ridge appears to have been formed in association with the sharply inset posterior fossa, an interpretation of the anterior fossa as an independently developed structure of the same status does not appear warranted.

The presence of the posterior fossa suggests muscular insertion.[2] However, judging from the characteristic relationship

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[2] The structure of the lateral surface of the angular in some gorgonopsians illustrated in the literature seems to contrast with the angular studied here. According to Brink and Kitching (1953, fig. 3) the posterior fossa in *Dinogorgon oudebergensis* is subdivided into two separate fossae. According to a photograph of the angular of *Lycosuchus* (?) published by Janensch (1952, pl. 16, fig. 3) the inferior margin of the anterior fossa is sharply defined by a well-developed ridge extending forward from the

between the structure of fossae and muscular attachment in modern vertebrates, as described above in the section on *Bauria,* it would not be expected that musculature descending from the anterior root of the zygomatic arch would have overlain the vertical ridge (VR, text-fig. 5B) and then inserted into this fossa; such is required under Parrington's hypothesis. The fossa, being marginless posterodorsally, supports a reconstruction of adductor jaw musculature originating from the posterior segment of the zygomatic arch. A muscle mass with a line of action as indicated in Text-figure 5B would have the same relationship to the anterior margin of the posterior fossa as does the zygomaticomandibularis muscle to the anterior margin of the masseteric fossa in modern mammals. In gorgonopsians, the posterior portion of the zygomatic arch seems to be a feasible area of muscular origin (despite much distortion in the specimens examined). The coronoid process of the dentary is placed far forward just medial to the arch at the level of the postorbital bar. In contrast to therocephalians, almost the entire length of the arch posterior to this level is available for muscular attachment assuming that such musculature gained sufficient fiber length by inserting on the lateral surface of the lower jaw.

If adductor jaw musculature of the type reconstructed in Text-figure 5B attached over the entire lateral surface of the posterior part of the angular in gorgonopsians, this condition would appear to be a specialization peculiar to a group which is currently believed to represent a phylogenetic "dead end". There is no structural basis for extrapolation of this arrangement from gor-

main ridge of the angular. This ridge gives the anterior fossa the appearance of an independently developed structure. Assuming that such variation is not an artifact of preservation or preparation, it ultimately may modify the reconstruction presented here for gorgonopsians if musculature was indeed responsible for the formation of these fossae. Conceivably musculature with a posteroventral source inserted into the inferior portion of the posterior fossa and adductor jaw musculature inserted into the anterior fossa. None of these possibilities, however, affects the general conclusions of this paper. There is no evidence for proposing that adductor musculature possibly inserting into the anterior fossa in gorgonopsians was present in the ancestry of cynodonts. In procynosuchids the reflected lamina is positioned just posterior to the dentary, eliminating the area represented by the anterior fossa; there is no sign that the posteroventral portion of the dentary was substituted as an area of muscle attachment.

gonopsians to other non-cynodont theriodonts (see discussion under *Bauria*). Of more importance, the structure of the reflected lamina in cynodonts suggests that the gorgonopsian arrangement of musculature was not present in this group either.

In the moderately advanced cynodont, *Thrinaxodon*, (pl. 1) the dorsal edge of the reflected lamina forms a horizontally oriented shelf set out laterally from the main surface of the lamina. This shelf forms the dorsal margin of a trough-shaped concavity, marginless posteroventrally, on the lateral surface of the lamina. Neither the shelf nor the concavity suggests that musculature descending from above inserted on the lamina. In addition, the lamina in cynodonts has no dorsal support for most of its length. In this respect its structure parallels that in *Bauria* and contrasts with that in gorgonopsians (cf. pls. 1, 4, and 5). This lack of support is difficult to reconcile with the reconstruction of adductor jaw musculature. Moreover, in order to postulate that the arrangement of adductor jaw musculature in gorgonopsians is pertinent to cynodonts (i.e., that cynodonts derived such an arrangement from a morphological stage exemplified by gorgonopsians) it is necessary to assume that the lamina lost its support at a right angle to the muscle pull and that the area of insertion was reduced by the formation of a significant gap between it and the area of origin (cf. pls. 1 and 5). There appears to be a more reasonable alternative for the function of the cynodont lamina than to attempt to interpret its function from the condition in gorgonopsians. The fact that the ventral margin of the lamina is drawn out posteroventrally into a thin knife edge (pl. 1) suggests to me that the lamina served as a process for the attachment of musculature with a posteroventral source (see p. 20).

It appears reasonable from this structural evidence that cynodonts were derived from animals showing the same fundamental pattern of muscular insertion and relationship of musculature to the zygomatic arch as was originally reconstructed for *Dimetrodon*. This similarity to *Dimetrodon* holds for either of the two groups currently considered as possibly closely related to the ancestry of cynodonts. Brink (1960) proposed that scaloposaurids are closely allied to procynosuchids. Romer (1961) preferred the descent of cynodonts from the more primitive theriodonts of the phthino-suchian type. At either level of therapsid development there was,

I believe, no significant difference from the *Dimetrodon*-condition
in the general arrangement of muscular insertion and general
relationship of musculature to the zygomatic arch.

The Evolutionary Development of External
Adductor Jaw Musculature in Cynodonts

Cynodonts are the second group of theriodont therapsids to
show evidence that adductor jaw musculature descended beneath
the zygomatic arch and inserted on the exposed lateral surface of
the jaw.

As Crompton (1963) has demonstrated, the most primitive
cynodonts, the procynosuchids, show morphological modifications
from which changes in the distribution of adductor jaw muscula-
ture from a more primitive condition can be inferred. In procyno-
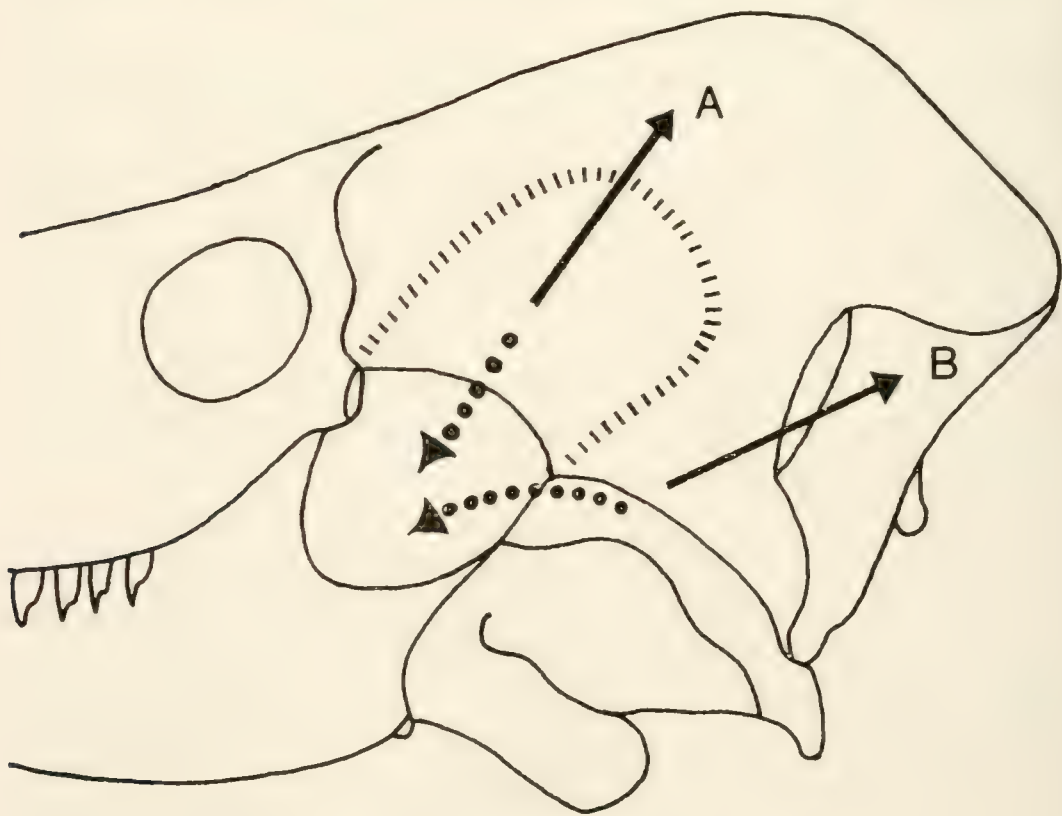
Text-fig. 7.   Lateral view of the skull of a procynosuchid illustrating
the possible sources (A and B) for the invasion of muscular attachment
onto the lateral surface of the dentary. The dashed line represents the
outline of the "bodenaponeurosis" reconstructed from a modern reptilian
model. (Skull outline modified from Broom.)

PLATE SECTION

Plate 1.   Above, stereophotograph of *Thrinaxodon* sp. (SAM specimen, unnumbered). Lateral view of the left reflected lamina of the angular and the posterior part of the left dentary. Below, *Dimetrodon milleri* (MCZ 1361). Lateral view of the right angular. Both, ×2.

Plate 2. Stereophotograph of *Thrinaxodon liorhinus* (UC 40466).
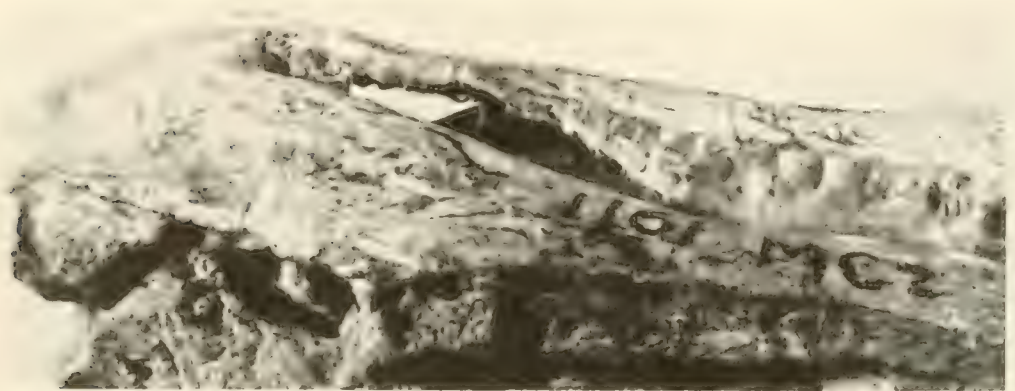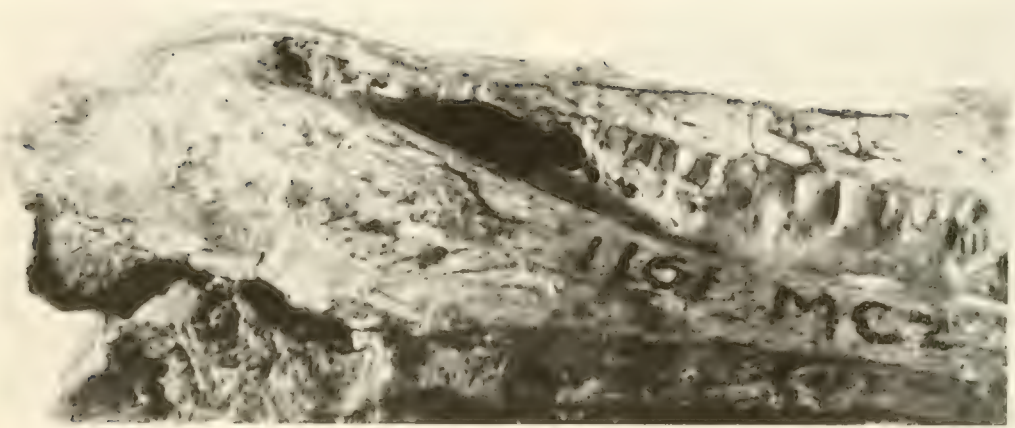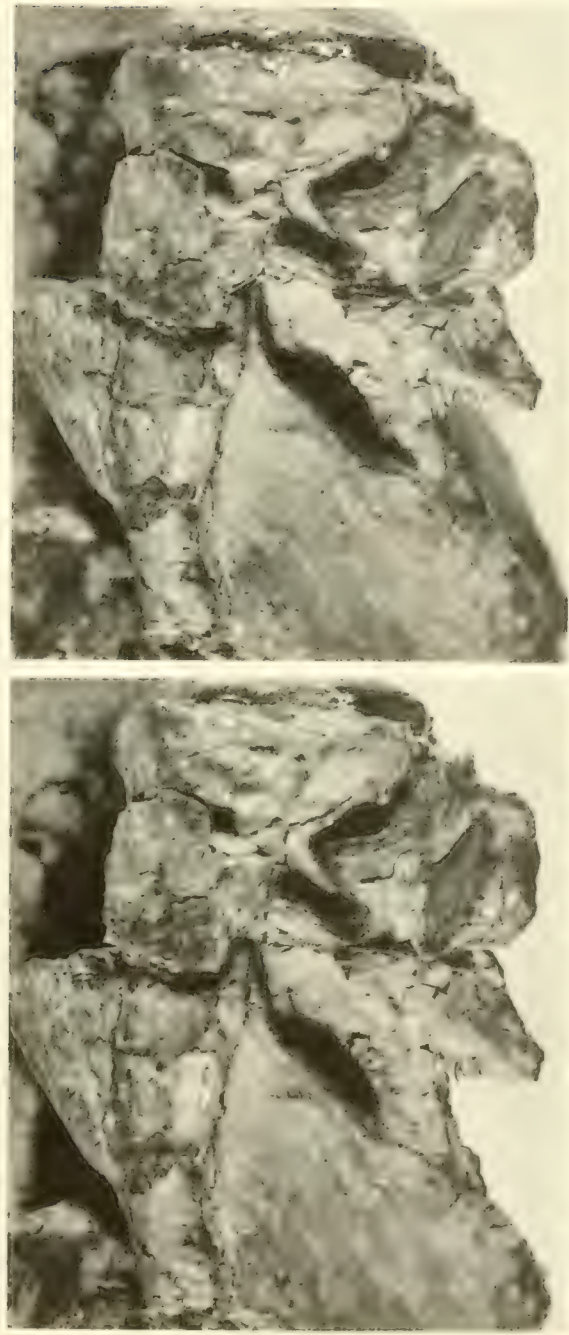Lateral view of the posterior part of the left side of the skull and
lower jaw. ×1.5.

Plate 3 (above). Stereophotograph of *Eothyris parkeri* (MCZ 1161). Ventral view of the right half of the skull and mandible. ×2.

Plate 4 (below). Stereophotograph of *Bauria cynops* (AMNH 5622). Lateral view of the posterior part of the left lower jaw. ×1.5.
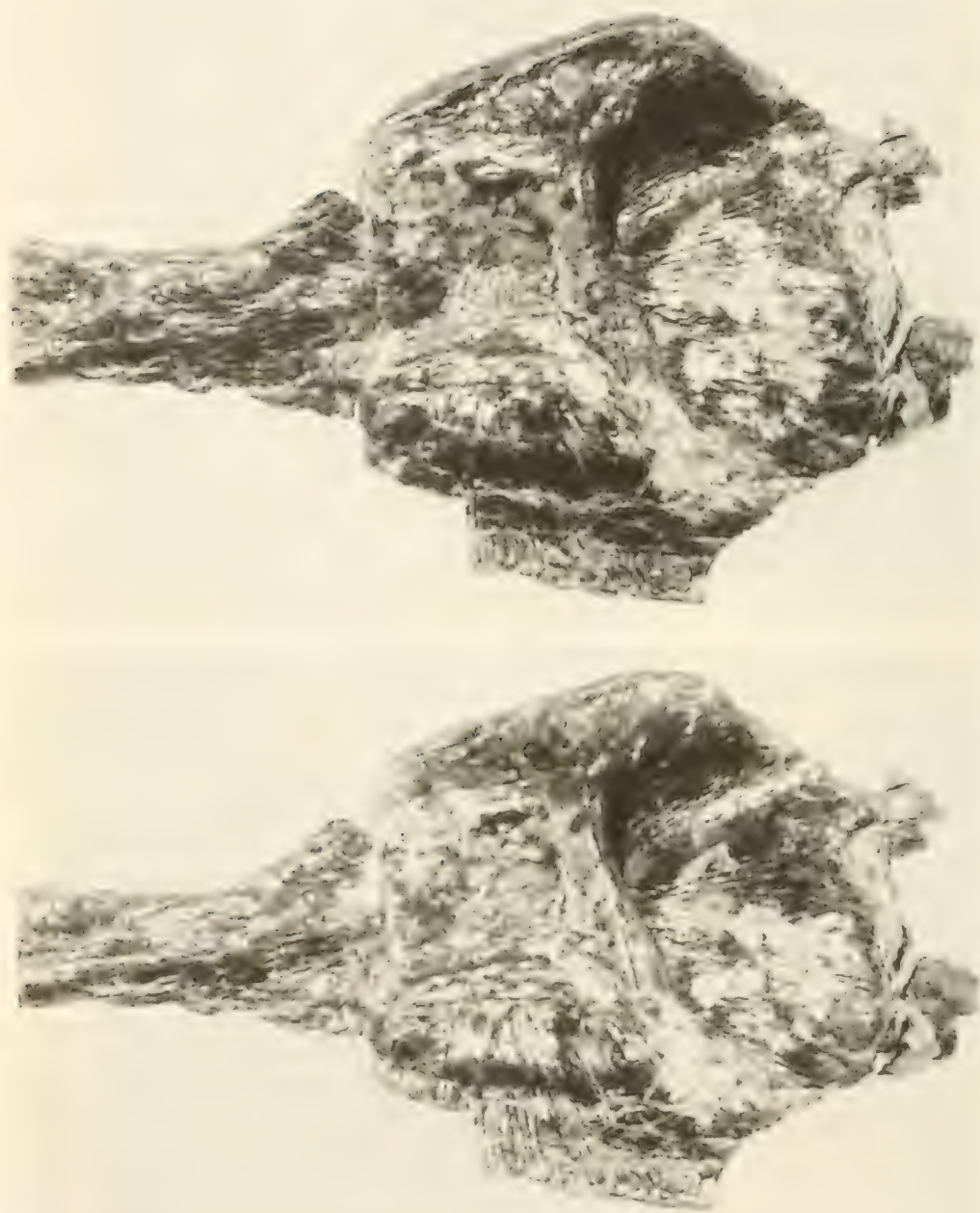
Plate 5. Stereophotograph of an unidentified gorgonopsian. Lateral view of the left angular. ×1.

Plate 6. Stereophotograph of *Trirachodon* sp. (SAM 12168). Lateral view of the posterior part of the left side of the skull and lower jaw. ×2.

suchids a fossa is found on the dorsolateral surface of the dentary (text-fig. 8B). As observed on the cast of the lower jaw of an unidentified specimen this fossa clearly reflects the attachment of musculature. In general shape and in the manner by which it is set off from the rest of the jaw, it is directly comparable to fossa development associated with the attachment of adductor jaw musculature in modern vertebrates (e.g., fossae which are associated with the insertion of M. adductor mandibulae externus superficialis in many turtles). The insertion of musculature in this position represents a distinct departure from the arrangement of the adductor jaw musculature in more primitive theriodonts. In the morphological stage of development represented by therocephalians and gorgonopsians muscular insertion in an equivalent position on the dentary was precluded by the close relationship between the zygomatic arch and the coronoid process (Crompton, 1963, p. 728) as illustrated in Text-figure 6. The intervention of musculature between the zygomatic arch and the dentary indicated by the fossa in procynosuchids was made possible because in all cynodonts the zygomatic arch is bowed outward away from the lateral surface of the jaw (cf. text-figs. 6 and 9).

There are two possible sources for the derivation of this procynosuchid muscle mass within the arrangement of the adductor externus musculature proposed for more primitive synapsids. The first possibility (A, text-fig. 7) is a derivation from that portion of the external adductor muscle originally reconstructed in *Dimetrodon* as arising from the undersurface of the temporal roof and inserting on the lateral surface of the "bodenaponeurosis" (represented by the anterior arrow, text-fig. 2). It appears reasonable that a muscular origin in similar position would have been maintained by the substitution of an aponeurotic sheet for the bone after the reduction of the temporal roof in therapsids. The anterior portion of the superficial component of the temporalis muscle in modern insectivorous, carnivorous and primate mammals has this type of origin from the undersurface of a temporal aponeurosis which superficially covers the temporal fossa (Temp Apon, text-fig. 10). Moreover, the presence of well-developed temporal, sagittal and lambdoidal crests in therocephalians and procynosuchids suggests the presence of such an aponeurosis (Temp Apon, text-figs. 13B and C) since in modern mammals

such crests are formed at the sites of attachment of the temporal aponeurosis to the skull as ossifications into the tendinous sheet itself (Scott, 1957). The derivation of the procynosuchid muscle from musculature formerly inserting on the lateral surface of the "bodenaponeurosis" would have required but a simple ventral extension of the area of insertion onto the lateral surface of the coronoid process subsequent to the bowing of the zygomatic arch.

As a second possibility (B, text-fig. 7) this musculature may have been derived from that portion of the external adductor reconstructed as arising from the posterolateral wall of the temporal fossa and inserting fleshily on the dorsal surface of the surangular in *Dimetrodon* (represented by the posterior arrow, text-fig. 2). With this hypothesis, the area of insertion would simply have been extended anteriorly onto the lateral surface of the procynosuchid dentary subsequent to the bowing of the zygomatic arch. This is the manner of invasion proposed by Crompton (1963) based on the fact that the floor of the procyno- suchid fossa is directly continuous with the dorsal surface of the surangular.

In procynosuchids themselves there are three possible areas of origin for that portion of the musculature inserting into the fossa on the dentary. They are: 1) the undersurface of a tem- poral aponeurosis (text-fig. 13C); 2) the posterior root of the zygomatic arch (from which the muscle mass arched forward to insert on the dentary as does the posterior portion of the super- ficial temporalis muscle in mammals); or 3) the medial surface of the zygomatic arch itself, as reconstructed by Crompton (1963, fig. 12). The last possibility points out another consequence of the bowing of the zygomatic arch; the lateral displacement of this structure opened the medial surface of the arch as a potential area of muscular origin. Even if there were no muscular attach- ment there in procynosuchids, such an area of origin had obviously been established in more advanced cynodonts (see p. 31).

In his discussion of the phylogenetic development of the cynodont jaw Crompton (1963) suggested that the muscle mass which initially inserted into the procynosuchid fossa retained its insertion in a dorsal position on the dentary in all later cynodonts. Accordingly he designated this musculature as a "deep masseter" muscle since under these conditions it would have occupied an

area of insertion roughly paralleling that of the deepest part of the masseter complex (or zygomaticomandibularis muscle which in this discussion is considered to be a medial component of the masseter muscle) in modern mammals. Following Parrington, Crompton reasoned that the insertion of another component of the masseteric musculature ("superficial masseter") was transferred from the reflected lamina and that the insertion of this musculature then occupied the ventral part of the lateral surface of the dentary in more advanced cynodonts where there is evidence that musculature attached down to the ventral edge of the posterior part of the dentary (see below).

The rejection of Parrington's conclusions, however, leads directly to another hypothesis. The fossa in procynosuchids does not reflect, as Crompton concluded, merely the migration onto the dentary of the insertion of a "deep masseter" muscle whose attachment then remained in this dorsal position. The fossa instead reflects the initial stage of a distinct anteroventral differentiation of external adductor musculature which ultimately developed into the entire cynodont masseter muscle.

In *Thrinaxodon,* which represents a more advanced morphological level of cynodont development than the procynosuchids, a masseteric fossa occupies the entire lateral surface of the posterior one-third of the dentary (text-fig. 8C). The presence of the fossa demonstrates, as is indicated by Crompton's interpretation of it as an insertional area, that musculature inserted all the way to the ventral edge of the posterior part of this bone (see text-fig. 13D). Consequently, this part of the dentary was established as a muscle-bearing ramus in mammalian fashion. The anterior limit of this fossa is a direct ventral continuation of the anteroventral margin of the coronoid process and marks a distinct change in surface relief from a convex surface anteriorly to a flat surface posteriorly (pl. 2), the latter surface forming the floor of the fossa. This change in relief has almost perfect qualitative correspondence to distinctions in surface topography found separating the body from the muscle-bearing ramus of the mandible in modern mammals. This change of topography marks the anterior limit of masseteric insertion. *Thrinaxodon,* therefore, shows the development of a muscle mass with relationships approaching those of the mammalian masseter muscle.
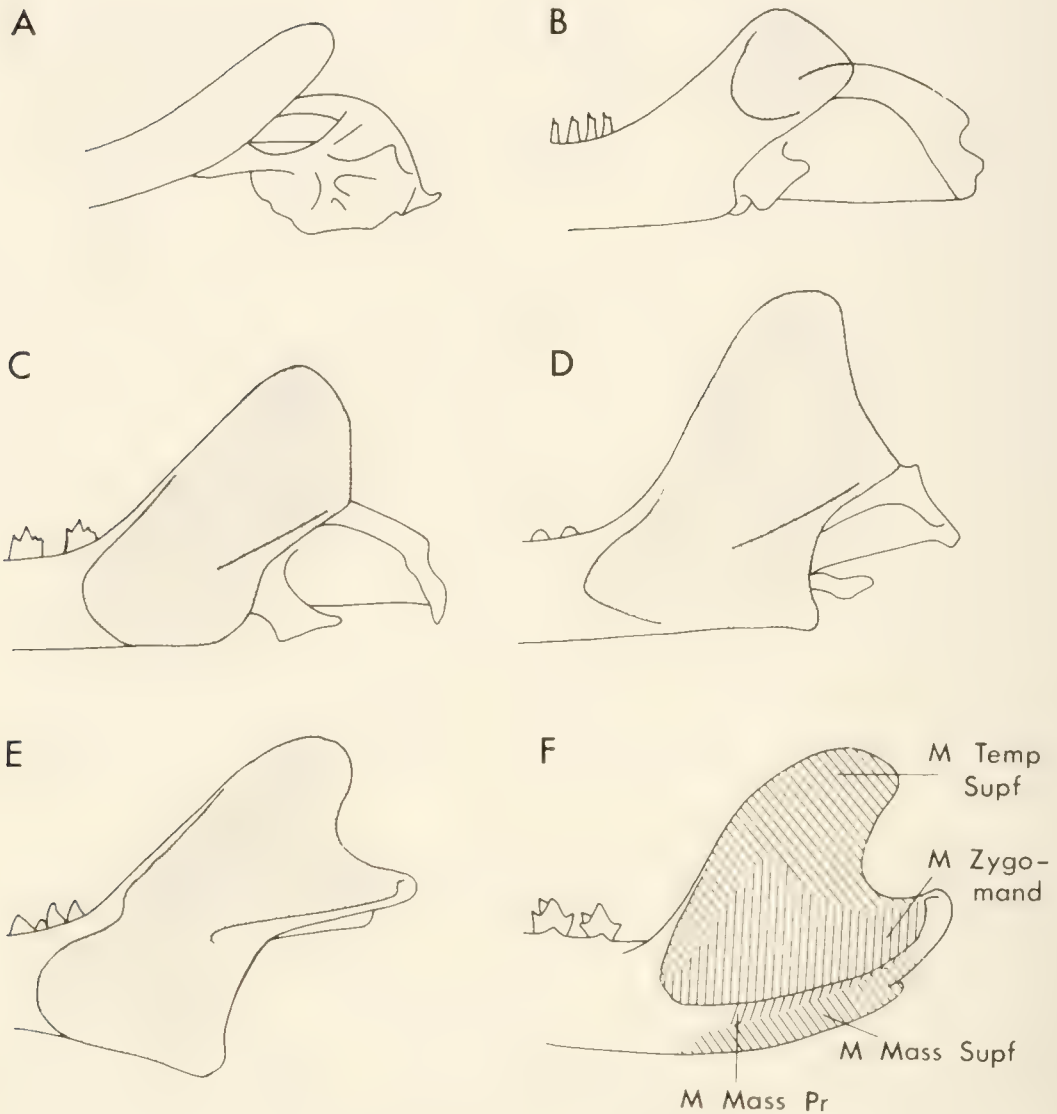
Text-fig. 8.   Lateral view of the posterior half of the lower jaw illus-
trating the extent of the floor of the masseteric fossa. A. the scaloposaurid
Ictidosuchops (for comparison, showing no fossa), B. a procynosuchid, C.
Thrinaxodon, D. *Trirachodon*, E. *Diarthrognathus*, F. *Didelphis* (for com-
parison, including a map of muscular insertions). The extent of the floor
of the masseteric fossa is indicated by stippling (B-E). In F the floor of
the fossa is continuous over the areas indicated for the insertions of
zygomaticomandibularis and superficial temporalis musculature. (Jaw out-
lines A-E after Crompton. Extent of the floor of the fossa in E based on
Crompton, 1963, fig. 1 and pl. 1A.) Not to scale.

In addition to the ventral extension of the fossa, *Thrinaxodon*
also illustrates an initial stage in the posteroventral expansion
of the cynodont dentary. The ventral portion of the ramus of the
dentary departs from that of a procynosuchid in showing a greater

relative posterior expansion at the expense of the lateral exposure of the postdentary bones (text-fig. 11A). The evidence in *Thrinaxodon* suggests that the development of masseter-like musculature was intimately related to and can account for the expansion of this portion of the dentary. The fact that the floor of the masseteric fossa is continuous over the posteroventral increment (text-fig. 8C; pl. 2) suggests strongly that the insertion of the cynodont masseter muscle included this new addition. This meets the expectation, derived from modern mammals (text-fig. 8F), that the entire floor of the masseteric fossa would have been occupied by muscle attachment.

Crompton (1963, fig. 11A) suggested that the musculature inserting on the ventral part of this fossa in *Thinaxodon* and more advanced cynodonts was derived from musculature inserting on the reflected lamina. In view of the conclusions reached here concerning the reflected lamina, the obvious alternative to Crompton's suggestion is that the musculature which inserted on the dorsal part of the lateral surface of the dentary in procynosuchids simply migrated ventrally to achieve the condition in *Thrinaxodon*. The cynodont masseter muscle is considered here to be a newly differentiated muscle mass not found in any other group of therapsids. Under this new hypothesis the developmental stage reached in *Thrinaxodon* reflects a great relative increase in the size of the cynodont masseter muscle concomitant with the increase in relative insertional area achieved by the ventral migration of muscular attachment and the expansion of this attachment over the posteroventral extension of the dentary.

In *Thrinaxodon* and more advanced cynodonts, the ventral and anterior extent of the masseteric fossa indicates that the origin of adductor jaw musculature was definitely established on the anterior part of the zygomatic arch. It is very difficult to imagine that musculature inserting on the anteroventral portion of this fossa would have its origin elsewhere. In addition, in some specimens of *Thrinaxodon*, a faint ridge possibly marking muscle attachment is found running along the inferior border of much of the length of the arch forward to the jugal-maxillary suture. Because of its similarity to the mammalian type relationship between the zygomatic arch and lower jaw, the morphology of *Thrinaxodon* (text-fig. 9) easily supports the reconstruction of

masseter-like musculature taking origin along the entire length of the medial surface of the arch (cf. text-figs. 9 and 10).

The trend for the enlargement of the ventral part of the dentary culminates in the *Cynognathus* zone cynodonts exemplified here by *Trirachodon* (SAM 12168, text-figs. 8D, 11B, pl. 6). The illustrated specimen shows the formation of a posteroventral angular region with a distinct angular process. In its entirety the
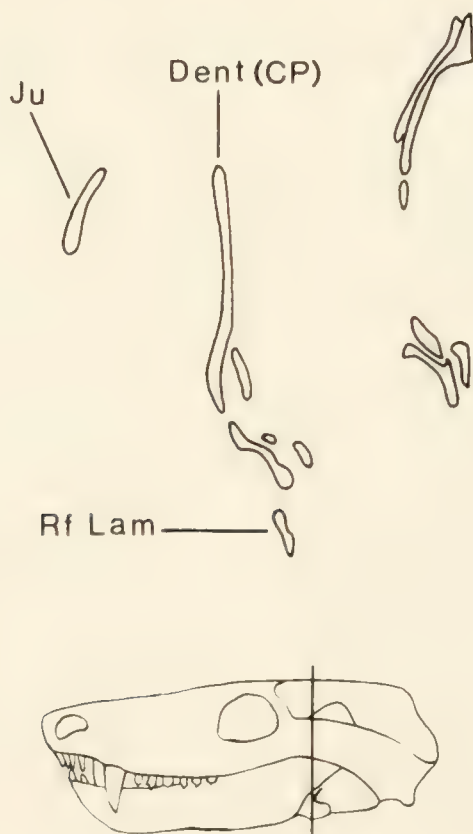

Text-fig. 9.   Transverse section through the temporal region in *Thrinaxodon* illustrating the relationship of the zygomatic arch to the coronoid process of the adducted jaw. (Modified after Fourie with the relationship between the jugal and dentary based on SAM 4282.)

angular region represents an increment over the outline of the dentary in *Thrinaxodon* (text-fig. 11B). Again, as in *Thrinaxodon*, the floor of the masseteric fossa is continuous over the entire ventral portion of the ramus including, in this case, the angular region. This continuity again strongly suggests the extent of the insertion of the cynodont masseter muscle and indicates that further development of the masseter-like muscle is reflected

in the formation of the angular region. The reconstruction of masseteric musculature attaching to the angular region in *Trirachodon*, indicated by this evidence, conforms with the conclusions of
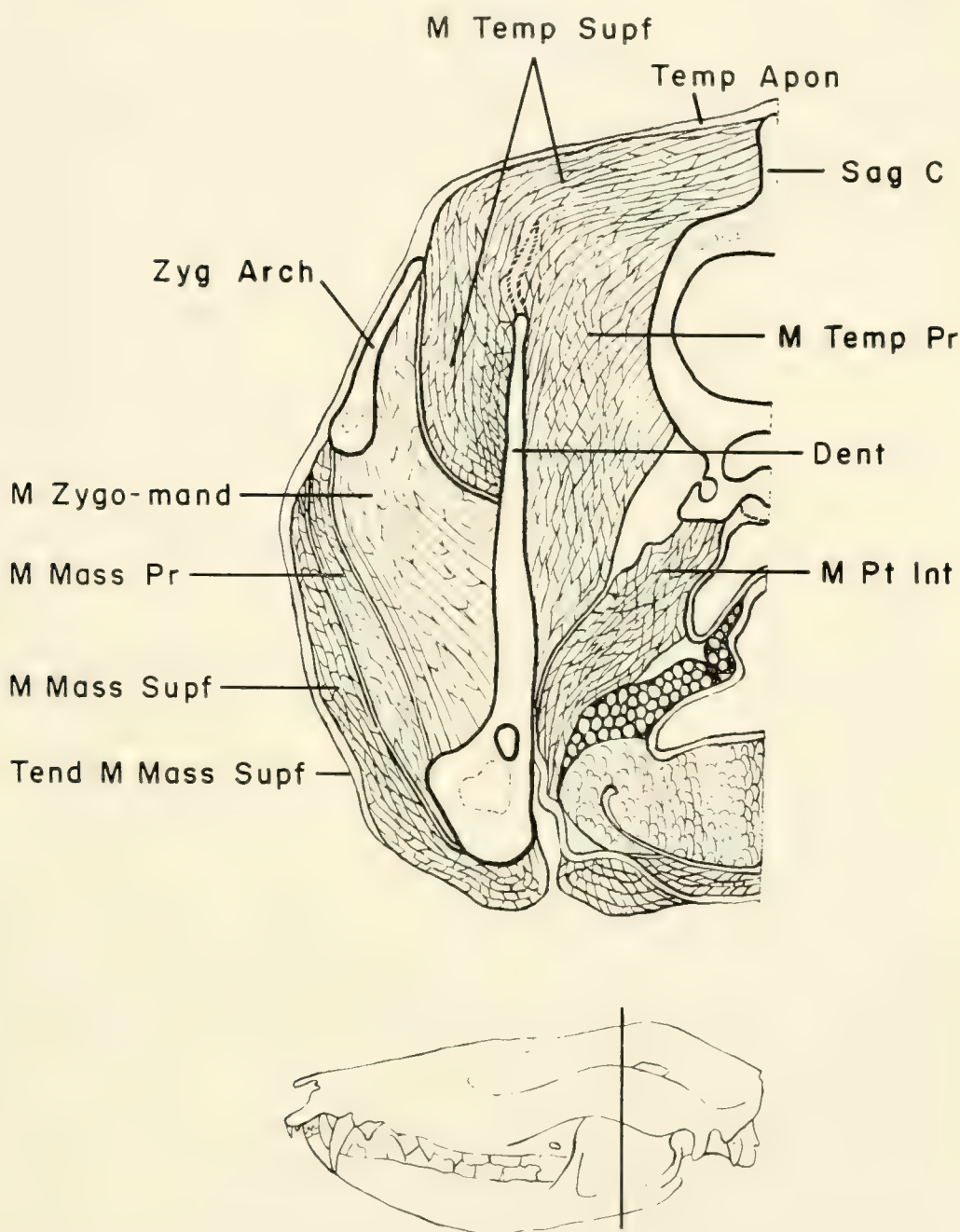
Text-fig. 10. Semidiagrammatic transverse section through the temporal region of *Didelphis*. The planes separating the zygomaticomandibularis from the profundus part of the masseter and the superficialis part of the temporalis are artificial. The portions of musculature thereby distinguished roughly correspond to masses commonly designated in this manner in many other mammals.
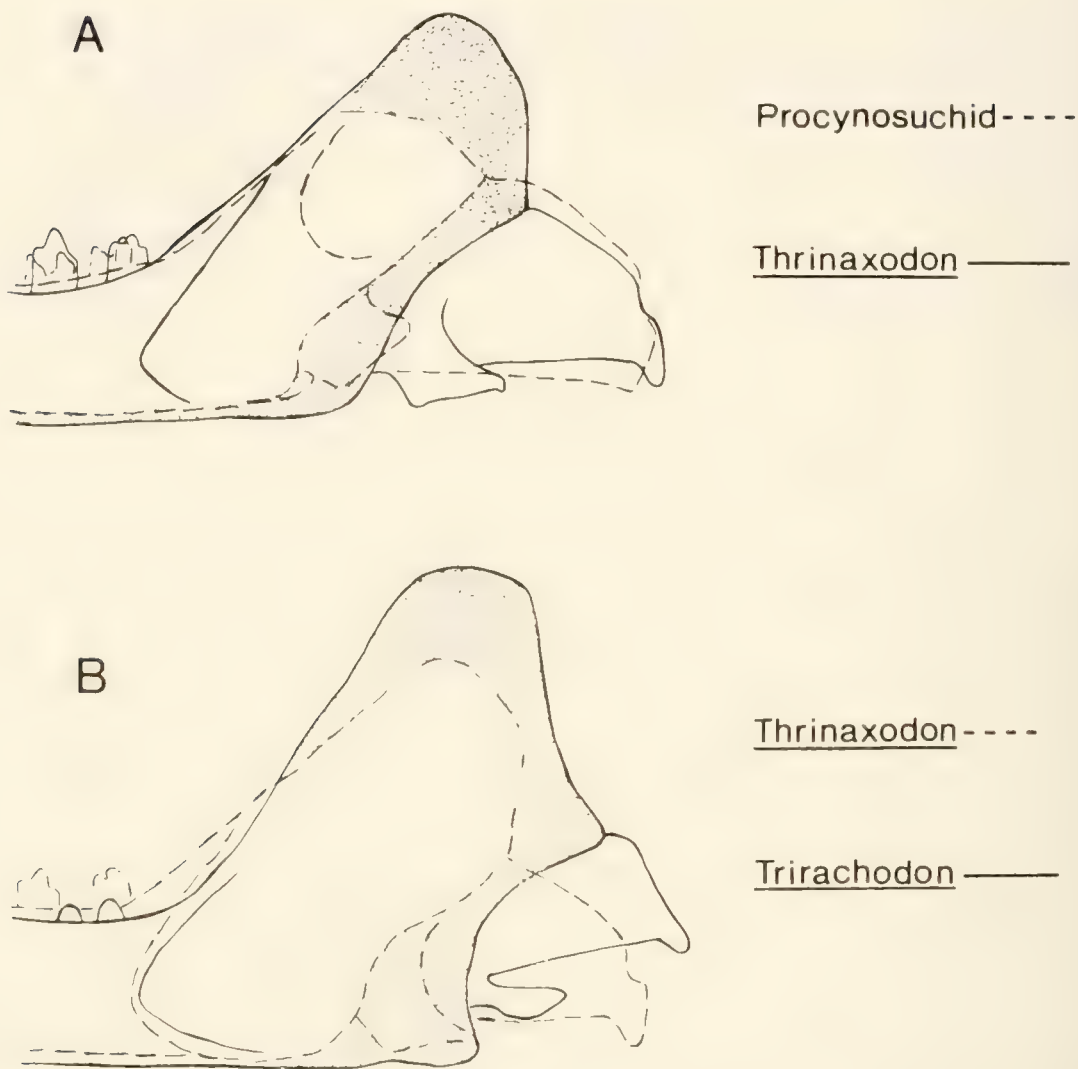
Text-fig. 11. Overlays of cynodont lower jaws illustrating stages in the relative expansion of the dentary. A. the jaw of a procynosuchid compared with that of *Thrinaxodon*. B. the jaw of *Thrinaxodon* compared with that of *Trirachodon*. The area of relative increment of the dentary is represented by stippling. The jaws are scaled to the same length measured from the symphysis to the jaw articulation. (Jaw outlines compared to specimens but redrawn from Crompton, 1963.)

Parrington (1955, 1959) and Crompton (1963) that such musculature inserted on the angle of advanced cynodonts and nontherian Mesozoic mammals in the same manner as in therian mammals. A similar extension of the floor of the masseteric fossa over the angle in *Diarthrognathus* (text-fig. 8E; also see Crompton, 1963, fig. 1B) and in docodontids (YPM 20992, 14620) indicates the probability that masseteric musculature attached to the angle in early nontherian mammals as well.

The reconstructions of Parrington and Crompton and the views expressed here contrast with the conclusions presented by Patterson and Olson (1961) on the function and development of the angular process in cynodonts. Elaborating on the initial conclusions of Patterson (1956), they suggested that: 1) the angular process of cynodonts and non-therian Mesozoic mammals is not homologous to the therian angle; 2) the cynodont angle served, by analogy drawn with the "echidna" angle of monotremes, for the attachment of a depressor muscle to the apparent exclusion of adductor jaw musculature; and 3) the expansion of the cynodont angle was correlated with the loss of the retroarticular process thus indicating a shift from reptilian to mammalian type depressor musculature. The evidence afforded by *Trirachodon* and the Mesozoic mammals cited, however, modifies the conclusions of these two authors. It appears certain that musculature attached to the cynodont angle; however, the extension of the masseteric fossa provides the one piece of suggestive evidence whereby the muscle mass involved can be readily identified. This evidence strongly suggests a relationship of the cynodont and nontherian angle to a masseter-like muscle irrespective of whether this angle is to be considered a cynodont and Mesozoic mammalian specialization or the homologue of the therian angle. Thus the "echidna" angle does not appear to be an appropriate analogue upon which to base a functional interpretation of this structure. Nor, in my opinion, does the "echidna" angle appear to be homologous to the cynodont and Mesozoic mammalian angle. The "echidna" angle may be a generic specialization for the attachment of a depressor muscle as the marginal process, sometimes present and sometimes absent at the site of insertion of the digastric muscle in therian carnivores, may also be. The evidence in cynodonts suggests that the formation of the cynodont angle cannot reasonably be considered to have been independent of the trend involving the expansion of the posteroventral portion of the dentary, related to the development of the masseter-like muscle, already well under way in more primitive cynodonts (text-figs. 11A and B). In the specific case of the angle, however, it appears that musculature other than the cynodont masseter also attached to this structure and must be considered in accounting for its formation. Crompton (1963, p. 718) described a muscle scar on the

posteromedial surface of the cynodont angle whose position indi-
cates the attachment of musculature with a ventral source. Con-
ceivably this might have been a depressor muscle, but if one accepts
Parrington's (1955) conclusion that the therapsid retroarticular
process served for the attachment of reptilian depressor muscula-
ture, the presence of the retroarticular process in cynodonts with
well-developed angular regions (see Crompton, 1963, figs. 5, 9,
and 10) points to the conclusion that pterygoideus musculature
attached to the medial surface of the angle,as Crompton suggested.

From the conclusion that the early cynodont stages represent
a period of differentiation and development of the cynodont mas-
seter muscle, there is no *a priori* reason to expect this muscle
mass to have been subdivided into deep and superficial compo-
nents as is the masseteric musculature of modern mammals. In
procynosuchids and *Thrinaxodon*, the position of the masseteric
fossa relative to the zygomatic arch, in the absence of other
specific evidence, suggests musculature with a posterodorsal fiber
direction (text-figs. 13C and D). In *Thrinaxodon* such muscula-
ture would roughly resemble the deep components (including the
zygomaticomandibularis muscle) of the mammalian masseter
muscle. In advanced cynodonts, however, evidence does exist
which suggests that the total organization of the muscle mass into
a condition approaching that of mammals has been achieved.
This includes the appearance of tubercles or flanges descending
ventrally from the jugal and the appearance of the angular process.
At this level of cynodont development I concur with Parrington
(1955, 1959) and Crompton (1963) that musculature topograph-
ically equivalent to the mammalian superficial masseter compo-
nent was present and attached to these structures (text-fig. 13E).

In advanced cynodonts where it is very probable that the
entire length of the zygomatic arch served as an area of muscle
origin, the protuberances from the jugal strongly suggest a con-
centrated tendinous muscle attachment anteriorly. In *Diademodon*
(see Brink, 1963, fig. 13) the flange descending ventrally from
the jugal resembles one in sloths on which a specialized heavy
attachment of masseter musculature occurs (Sicher, 1944). The
shape and position of smaller tubercles found in *Trirachodon*
(pl. 6) and *Cynognathus* closely resemble those found in *Erina-
ceus* and *Solenodon,* among modern insectivores, in which these

structures mark the position of a concentrated tendinous attachment of the superficial component of the masseter muscle. The coincidental appearance in advanced cynodonts of tubercles and flanges indicating a concentrated masseter origin anterodorsally and of the angular process of the dentary for masseter insertion posteroventrally suggests that relating the two areas of attachment to a single muscle mass is a reasonable possibility. If this relationship is made, the cynodont masseter at this level of development can be viewed as being organized into components the most lateral of which possessed fibers with a posteroventral direction and which had, at least in part, the relations of the superficial component of the mammalian masseter muscle (text-fig. 13E).

In cynodonts, the acquisition of a mammalian type of adductor jaw musculature probably involved more than the differentiation and development of a masseter-like muscle. The coronoid process shows progressive dorsal and posterior expansion resulting in the development of broad lateral and medial surfaces (text-fig. 11). Beginning at the *Thrinaxodon* level of development this process resembles that of modern carnivorous and many insectivorous mammals. In contrast, the coronoid process in therocephalians and gorgonopsians is much more restricted in extent and has already been interpreted as serving for the attachment of a "bodenaponeurosis" as in modern reptiles. Presumably, a "bodenaponeurosis" also attached to the abbreviated coronoid process in procynosuchids (text-fig. 7). In more advanced cynodonts, however, comparison with the mammals already cited indicates the development of a different arrangement of muscular insertion. The broad medial surface of the coronoid process would be expected to have served for the fleshy attachment of deep temporalis fibers (as illustrated in transverse section in *Didelphis*, text-fig. 10, and by maps of muscle attachment, text-figs. 3B and D). The lateral surface, medial to and above the zygomatic arch, probably served for the insertion of superficial temporalis fibers arising from the posterior root of the zygoma and the undersurface of a temporal aponeurosis (text-figs. 10 and 8F). Laterally, the structural correspondence with mammals is complete in cynodonts; the bowed zygoma allows for the insertion of the superficial components of the temporalis muscle (cf. text-figs. 9 and 10) and the continuity of the floor of the masseteric fossa

over the lateral surface of the process suggests it (cf. text-figs. 8C, D, and F). Following the conclusions presented here, the expansion of the coronoid process in cynodonts would represent a replacement of an aponeurosis by bone. Those fibers of the external adductor presumably attaching to the lateral surface of the "bodenaponeurosis" at a more primitive level of theriodont development would have achieved, through this modification, an area of insertion characteristic of the superficial temporalis component in modern mammals. External adductor fibers attaching to the medial surface of the aponeurosis would have attained an insertion characteristic of the deep temporalis component of modern mammals (text-fig. 3B).

If Crompton's (1963) reconstruction of the partial insertion of pterygoideus musculature on the angular process is accepted, then, as far as can be determined from the direct evidence presented and from analogy with modern mammals, cynodonts acquired detailed similarities to mammals in the organization of the insertion of all major components of the adductor jaw musculature. As it is viewed here, the enlargement of the dentary then reflects a major shift from a more primitive and reptilian muscular arrangement which involved the appearance of a masseter muscle, the reorganization of the insertion of external adductor musculature into that characteristic of M. temporalis and, as Crompton suggested, partial transfer of the insertion of pterygoideus musculature onto the angle. Cynodonts are the first and, as far as is known, the only theriodonts to effect these modifications.

The total mammalian pattern of muscular distribution is never completely achieved in therapsids. The origin of the pterygoideus musculature is believed to be, in large part, persistently reptilian throughout and to be basically similar to that reconstructed in *Thrinaxodon* (text-fig. 12A). As long as the accessory jawbones play a role in the formation of the lower jaw, the possibility remains that reptilian components such as the adductor posterior, the pseudotemporalis, and the pterygoideus musculature (text-fig. 3B) were present and inserting in reptilian fashion. Those portions of the adductor jaw musculature that did achieve a mammalian pattern of distribution as reflected in the evolution of the therapsid skull and jaw, did so in a mosaic pattern of evolutionary development. As far as I can determine, that part

of the jaw musculature arising from the dorsal and posterodorsal parts of the temporal fossa attained (perhaps independently) an area of origin closely approaching that of the mammalian temporalis muscle in the ancestry of therocephalians and cynodonts. In cynodonts this was combined with the modifications described above to produce a much closer approach to a mammalian type of adductor jaw musculature.

MAMMALIAN ORIGINS AND ADDUCTOR JAW MUSCULATURE

Since cynodonts show a major shift leading directly toward the establishment of a mammalian feeding mechanism and since they also hold a number of other characteristics in common with the earliest of mammals, there are strong reasons for re-examining the concept that some or all mammals were descended from bauriamorphs as opposed to cynodonts (see Romer, 1961). Crompton (1958) suggested that a specific group of early mammals, the ictidosaurs, were directly derived from bauriamorphs. He proposed that *Diarthrognathus* (a mammal by the criterion of a dentary-squamosal articulation) arose from scaloposaurids. With the evidence presently available a good case can be made, I believe, for a different interpretation; that is, that *Diarthrognathus* was derived from cynodonts.

Crompton's descriptions of the skull and jaws of *Diarthrognathus* leave little doubt that if this animal was directly descended from a scaloposaurid, the hypothetical intermediate forms must have established a skull and jaw morphology closely paralleling that of cynodonts. All of the modifications of the zygomatic arch and dentary from which the appearance and development of the masseter muscle and the establishment of a characteristic mammalian insertion for the temporalis muscle can be inferred must have evolved in parallel with these same modifications in cynodonts. Scaloposaurids (or any other bauriamorph) show none of these modifications (text-fig. 8A; see also Crompton, 1955, figs. 1 and 2B). *Diarthrognathus*, on the other hand, shows them all (text-fig. 8E; see also Crompton, 1958, fig. 6A; 1963, p. 703, fig. 1B). Thus the transitional forms leading to *Diarthrognathus* must have passed through the same general stages in the same sequence as is known to have occurred in cynodonts. The intermediates would also have had to reduce the accessory jaw bones

and establish a lateral flange of the prootic bordering the pterygo-paroccipital foramen. Both features are found in cynodonts, among therapsids, and shared by them with the earliest of mammals (see Crompton, 1958, and Hopson, 1964). In addition, the following modifications given by Crompton (1958, p. 210) as necessary for the development of *Diarthrognathus* from scaloposaurids, while not unique to cynodonts, are nevertheless found in them: expanded epipterygoid, elongated quadrate ramus of the epipterygoid, double occipital condyles, and no suborbital vacuities.

While parallelism has commonly been proposed in therapsid evolution, in this case it is very doubtful that it is justified. In the first place, there is an extensive amount of parallelism with cynodonts that must be postulated. In the second place, at least two of the three characteristics which are held by *Diarthrognathus* in common with scaloposaurids and which Crompton emphasized in drawing his phylogenetic relationships do not seem to offer serious obstacles to the derivation of *Diarthrognathus* from cynodonts. These three characteristics are: 1) presence of an interpterygoidal vacuity, 2) contact between the quadrate and paroccipital process, and 3) arrangement of the basipterygoid joint.

The procynosuchid *Leavachia* (Brink, 1963b, fig. 10) possesses fairly well-developed interpterygoidal vacuities. *Diarthrognathus*, conceivably, was descended from a group of unknown cynodonts retaining this configuration. There is, however, another alternative. The obliteration of the vacuity in moderately advanced cynodonts appears to be directly related to the influence of pterygoideus musculature. Estes (1961, p. 174, fig. 2) described juvenile specimens of *Thrinaxodon* with interpterygoidal vacuities bordered laterally by a ridge formed by the pterygoid (text-fig. 12C). During ontogenetic development this ridge (Med Pt Crest, text-fig. 12A) enlarges and migrates medially until it almost reaches the midline so that in adult specimens the interpterygoidal vacuity is covered ventrally. Estes suggested that the elimination of the vacuity was produced by the ontogenetic development of pterygoideus musculature. This seems to be the most likely explanation for the following reasons. Text-figure 12 shows a reconstruction of pterygoideus musculature in *Thrinaxodon* based on the condition in *Iguana* (cf. text-figs. 12A and B). There is a close correspondence between the medial pterygoid crest in *Thrinaxo-*
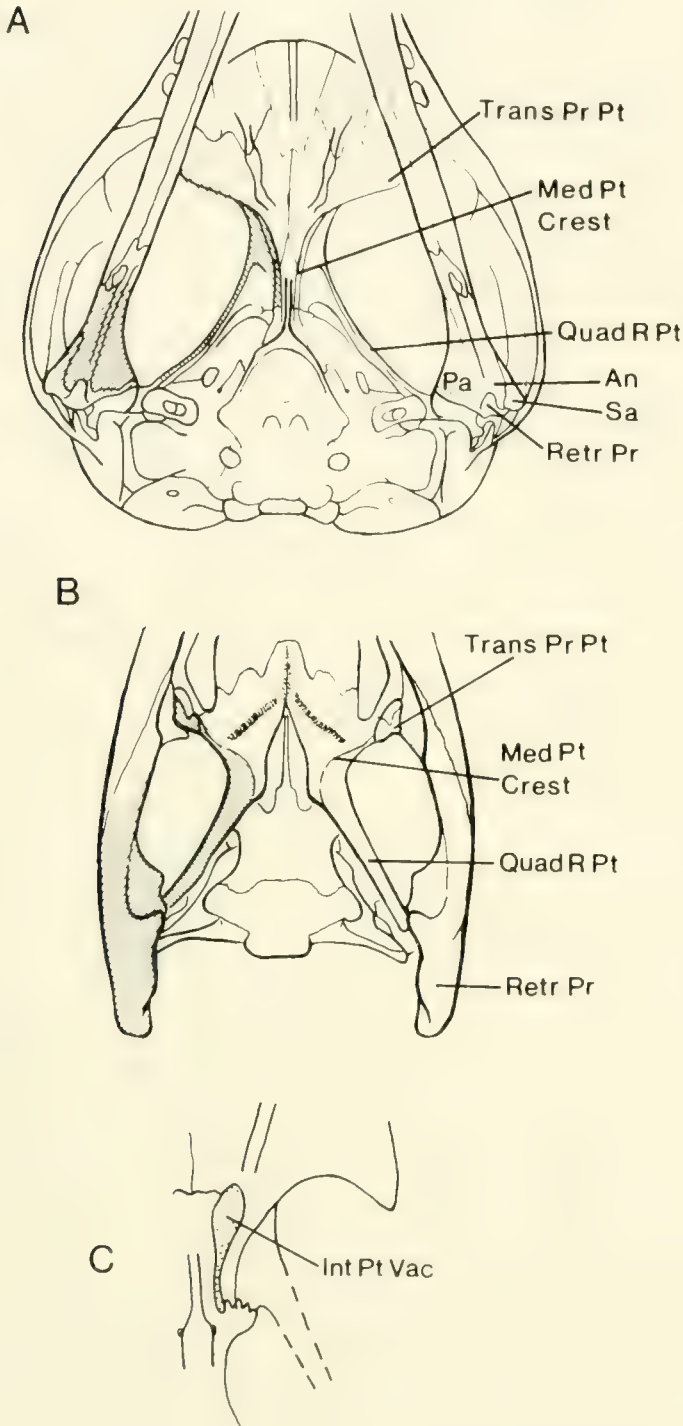
Text-fig. 12. A. ventral view of the posterior part of the skull and lower jaws of *Thrinaxodon*, B. a similar view of *Iguana*, C. ventral view of the left pterygoid region in a juvenile *Thrinaxodon*. The reconstruction of the origin and insertion, indicated by parallel lines, of pterygoideus musculature in A is based directly on the arrangement in B. The extent of the interpterygoidal vacuity in C is based on UC 42877. Not to scale.

don and a slightly raised ridge (Med Pt Crest, text-fig. 12B) extending posteromedially from the transverse process in *Iguana*. In *Iguana* and other living reptiles the transverse process and the medial pterygoid crest (when present) serve as the site of attachment for the aponeurosis of the pterygoideus muscle mass; the remaining area of origin in *Iguana* indicated in Text-figure 12B is in large part a fleshy attachment. The structural similarities suggest that the transverse process and the medial pterygoid crest served for aponeurotic attachment in *Thrinaxodon*. The ontogenetic behavior of this ridge in *Thrinaxodon* is in large part analogous with the migration of temporal crests during the ontogenetic development of the temporalis musculature in modern mammals (see Scott, 1957). As the migration of the temporal crests to the midline (to form a sagittal crest) in some modern mammals reflects an increase in size of the temporalis muscle and an emphasis on its medial attachment, the complete migration of the pterygoid crest to the midline in *Thrinaxodon* suggests the development of a large pterygoideus muscle also with emphasis on its medial attachment. However, in *Diarthrognathus* the developmental pattern and resulting adult configuration of the pterygoideus musculature may well have been different. A reestablishment of wide interpterygoidal vacuities in *Diarthrognathus* could have easily been produced from the condition in *Thrinaxodon* if the attachment of the pterygoideus musculature did not migrate medially. There is a considerable amount of variation between different adult mammals in the position of the temporal crests and whether or not they ultimately migrate medially to form a sagittal crest; this reflects variation in the size and or emphasis on different areas of origin of the adult temporalis muscle. A reduction in size of the pterygoideus musculature in *Diarthrognathus* as a modification beyond a morphological level represented by *Thrinaxodon* could account for the fact that the vacuities are again found in the adult. Such a reduction is possibly reflected in the diminished size of the transverse process and accessory jaw bones as described in *Diarthrognathus* by Crompton (1958).

The fact that *Diarthrognathus* apparently possesses a contact between the paroccipital process and the quadrate also does not seem to preclude the derivation of that form from cynodonts. According to Crompton (1964, p. 78, figs. 9 and 15) the quadrate

is partly suspended from the paroccipital process in *Leavachia*. This fact allows the possibility that unknown descendant groups of cynodonts retained such an arrangement rather than excluding it by the growth of an anterior flange of the squamosal as is found in *Lystrosaurus* and *Cynognathus* zone cynodonts (see Crompton, 1964). In addition, the fact that both *Oligokyphus* (see Crompton, 1964) and *Bienotherium* (see Hopson, 1964) apparently reestablished a contact between the paroccipital process and quadrate indicates that this possibility also exists for the descent of *Diarthrognathus* from cynodonts.

According to Crompton (1958), *Cynognathus* zone cynodonts appear far too specialized to be ancestral to *Diarthrognathus*. These specializations include: 1) the reduction of the quadrate rami of both the pterygoid and epipterygoid, 2) the massively developed external auditory meatus, and 3) the pattern of tooth replacement (gomphodonts). However, at present it is much more doubtful that a cynodont at or slightly above a level of development represented in large part by *Thrinaxodon* would be too specialized. Unless the nature of the basipterygoid articulation in *Diarthrognathus* and or conceivably new information on tooth morphology should prove to be insurmountable obstacles, available *Lystrosaurus* zone cynodonts seem to represent a general morphological level of development from which *Diarthrognathus* in particular and, at this stage in our knowledge, mammals in general could easily have been derived. The weight of evidence, centered on the evolution of adductor jaw musculature, is in their favor. In the absence of definite evidence to support it, the concept of the polyphyletic origin of mammals from widely divergent groups of theriodont therapsids may not be correct.

SUMMARY

Parrington's hypothesis of the evolutionary origin and development of masseteric musculature does not conform with the generalized relationship between the cheek and jaw in captorhinomorph and pelycosaur reptiles and is contradicted by the structure of the reflected lamina of the angular in sphenacodont pelycosaurs and theriodont therapsids.

The external adductor jaw musculature in most living reptiles is characterized by a fleshy insertion to the dorsal, dorsolateral
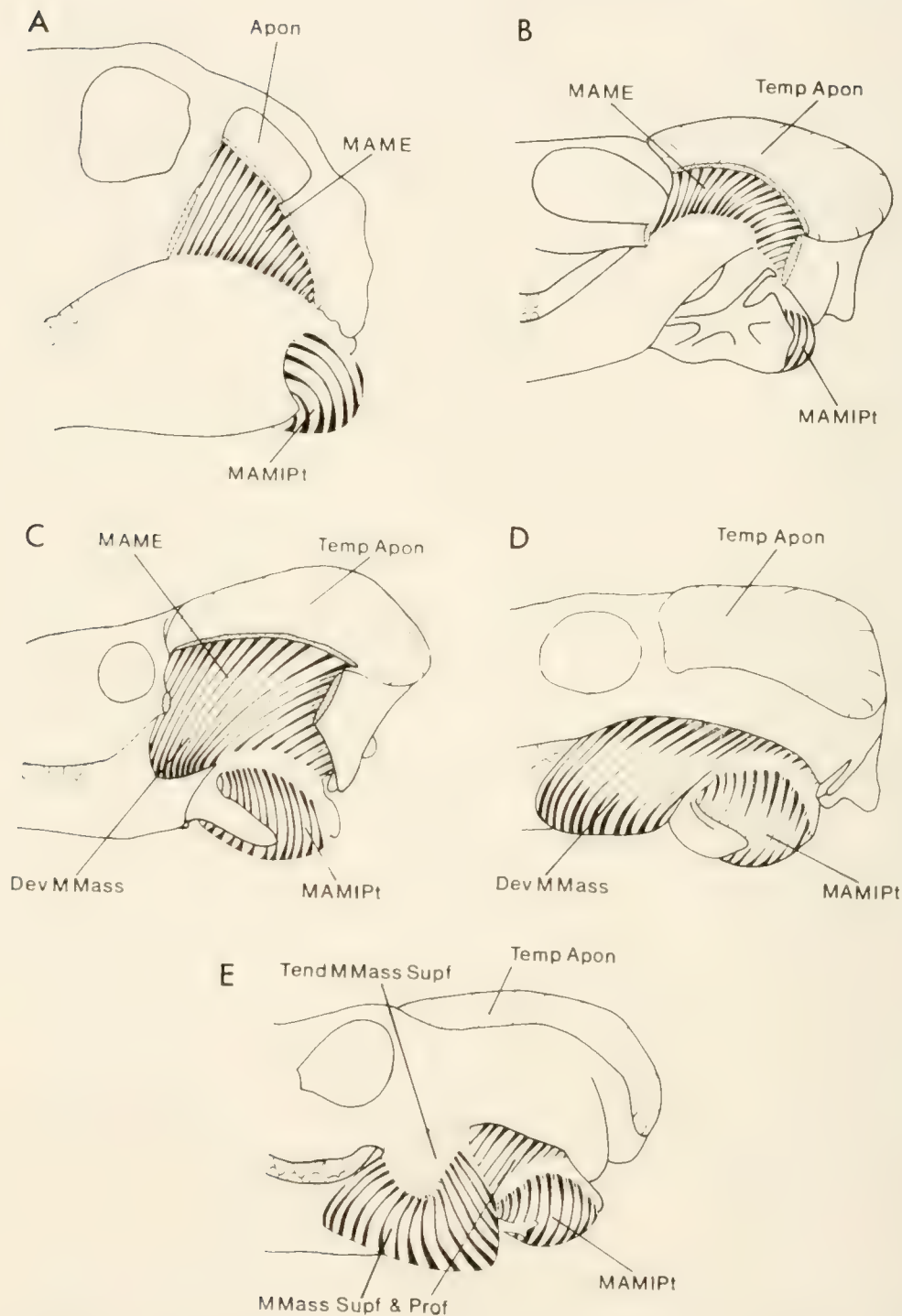
Text-fig. 13. A series of muscle reconstructions illustrating the primitive synapsid arrangement of external adductor jaw musculature and the method of evolutionary development of the cynodont masseter muscle as proposed in the text. A. *Dimetrodon*, B. *Bauria*, C. a procynosuchid, D. *Thrinaxodon*, E. *Trirachodon*. In A, B and C the zygomatic arch is removed. The arrangement of musculature in B is believed to represent a morphological stage directly antecedent to that in C. In C it is assumed that the zygomatic arch had not yet been established as a site of muscle attachment and the area of origin of the developing masseter muscle was the undersurface of a temporal aponeurosis. (Skull and jaw outlines in A after Romer and Price; in C after Broom.) Not to scale.

and dorsomedial surfaces of the posterior part of the lower jaw and by a concentrated attachment of a "bodenaponeurosis" to the coronoid region. The morphology of *Dimetrodon* is consistent with the reconstruction of this type of insertion except that there probably was little if any muscular attachment to the dorsolateral surface of the jaw (text-fig. 13A). It appears probable that no adductor jaw musculature descended beneath the level of the zygomatic arch to insert on the exposed lateral surface of the lower jaw. The distribution of the area of origin of external adductor jaw musculature in *Dimetrodon* also agrees with that in living reptiles insofar as it is likely that the medial surface of the inferior portion of the cheek, specifically the medial surface of the zygomatic arch, did not serve for the attachment of adductor jaw musculature.

Osteological modifications in two descendant groups of theriodont therapsids suggest that each group independently modified the pattern of distribution of external adductor musculature proposed for *Dimetrodon*.

Gorgonopsians appear to have been specialized among synapsids in that the insertion of jaw musculature migrated downward onto the posterior part of the lateral surface of the angular including the reflected lamina. Consequently it is likely that the origin of such musculature was established on the posterior part of the zygomatic arch.

In cynodonts (text-figs. 13C, D and E), which are believed to have been directly derived from animals which had the same pattern of muscular insertion as *Dimetrodon* and which did not have adductor musculature arising from the zygomatic arch (text-fig. 13B), there were two major changes. These modifications were intimately related to the expansion of the dentary and constitute a major shift from a reptilian to a mammalian pattern of external adductor musculature. The first major modification is that a masseter-like muscle differentiated from the external adductor. In primitive cynodonts (text-fig. 13C) the insertion of musculature invaded the lateral surface of the dentary subsequent to the bowing of the zygomatic arch. In more advanced cynodonts (text-figs. 13D and E) this insertion migrated downward to the postero-ventral edge of the dentary. In *Lystrosaurus* and *Cynognathus* zone cynodonts (text-figs. 13D and E respectively), if not before,

the zygomatic arch had been established as the area of origin of this musculature. It is probable that the masseter-like muscle of *Cynognathus* zone cynodonts achieved detailed similarities with the subdivision and distribution of the masseter muscle in living therian mammals. The second major modification is reflected in the posterodorsal expansion of the coronoid process of the dentary. This event indicates that the concentrated attachment of the "bodenaponeurosis" to the coronoid region, characteristic of the insertion of the external adductor in reptiles, was replaced, in *Lystrosaurus* and *Cynognathus* zone cynodonts, by a broad fleshy attachment on both sides of the expanded coronoid process. The latter is characteristic of the insertion of the temporalis muscle in living therian mammals.

The acquisition, in cynodonts, of adductor jaw musculature which closely approaches that in mammals and the related establishment of the posterior part of the dentary as a muscle bearing ramus provide strong grounds for reevaluating the concept that some or all mammals were derived from bauriamorphs. For these and other reasons cynodonts appear to be the best candidates for the ancestors of all mammals.

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Addendum

After reviewing the reconstructions made in the text, Dr. A. W. Crompton (personal communication) has suggested the possibility that a slip of the external adductor muscle migrated out from under the posterior part of the zygomatic arch at a post-pelycosaurian stage of evolution (the possibility of an escape route in early therapsids is suggested by a definite gap existing between the posteriormost part of the zygomatic arch and the lower jaw in gorgonopsians and therocephalians). In early therapsids it would have inserted on the dorsolateral surface of the posterior part of the angular superior to the contact between the body of the angular and the reflected lamina. This area is represented by the deep part of the posterior fossa in gorgonopsians and the gap between the angular crest and the free dorsal edge of the reflected lamina in *Bauria* (see text-figs. 5A and B). Subsequently, in gorgonopsians, this insertion would have migrated down over the reflected lamina and achieved the distribution reconstructed

in Text-figure 5B. In other therapsids, however, it may have been retained in dorsal position occupying the area represented by the gap in *Bauria* and therocephalians in general. While this hypothesis has not been incorporated into the reconstructions made in this paper it may prove to have considerable merit. It has the advantage of accounting for the structural similarities between the deep part of the posterior fossa in gorgonopsians and the gap in *Bauria*. Both have the same orientation and occupy the same relative position. In addition, it is conceivable that such an insertion could have cut through the contact between the body of the angular and the reflected lamina and thus account for the posterodorsal separation of the lamina from the body as is seen in therocephalians (cf. text-figs. 5A and B). Without this hypothesis the explanation of the gap and free dorsal edge of the reflected lamina in therocephalians represents a major enigma in the structural evolution of the angular.

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