THE EVOLUTION OF THE MAMMALIAN JAW

A. W. Crompton
South African Museum, Cape Town

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Recently a detailed study of the lower jaws of mammal-like reptiles was undertaken. The present paper is a summary of the conclusions reached as a result of this study. The full text has been published elsewhere (Crompton, 1963).

It has been known for many years (Broom, 1932) that it is possible to observe in the mammal-like reptiles, and especially in the therocephalians and cynodonts, a progressive increase in the size of the dentary and progressive decrease in the size of the accessory jawbones. Consequently, the jaw joint formed by the articular and quadrate became progressively weaker until in the early mammals such as *Morganucodon* (Kermack and Mussett, 1958, 1959a and b) and *Diarthrognathus*[1] (Crompton, 1958) a new mammalian joint was established between the dentary and the squamosal, and the primitive reptilian jaw joint formed only a small part of the composite jaw joint. The decrease in size and strength of the reptilian jaw joint in the cynodonts, for example, was accompanied by an increase in the mass of the jaw-closing musculature and consequently an increase in the strain to which the lower jaw was subjected. Many attempts (Watson, 1912; Adams, 1919; Parrington, 1934) have been made to explain the apparent enigma of an increase in the mass of the jaw-closing musculature, on the one hand, and a progressive weakening of the jaw joint on the other. No one of these explanations is entirely satisfactory.

In the study of mammal-like reptiles and mammal jaws an attempt was made to determine the areas of origin and insertion of the jaw-closing muscles at different evolutionary levels in order to determine the forces to which the jaw joint was subjected.

[1] In the original description (Crompton, 1958) I classified *Diarthrognathus* as a therapsid. However, since *Diarthrognathus* has an articulation between the dentary and the squamosal I have decided to follow Kermack and Mussett (1958) and Simpson (1959) and regard it as a mammal.

Cotylosaurs

In cotylosaurs (fig. 1A) the main jaw-closing muscle, the capiti-mandibularis (C.M.) (posterior adductors of Olson, 1961) was probably poorly differentiated and inserted in the adductor fossa. This was situated approximately midway between the glenoid and the posterior teeth. The direction of the fibers of the capiti-mandibularis was probably on an average vertical. Part of the adductor mass presumably inserted on the ventral surface of the lower jaw below the glenoid. This part was probably homologous with the pterygoideus musculature of more advanced forms. The upward thrust (C.M.) caused by these muscles was balanced by a vertical downward thrust (R) through the quadrate onto the articular, and a vertical downward thrust (B) (bite force) through the upper dentition onto the lower dentition. In cotylosaurs such as *Labidosaurus* the downward thrust through the quadrate (R) was as great as the downward thrust through the teeth (R). The direction of pull of the capiti-mandibularis appears to have formed a right angle with a line connecting the adductor fossa to the glenoid. Consequently, this muscle was most efficient when the jaws were closed, i.e., in this position the leverage was greatest. Because of the large vertical forces acting through the jaw joint in these forms, a reduction in the bones forming the jaw joint would not have been possible. This accounts for the large size of the bones forming the jaw joint in these forms.

Pelycosaurs

In the pelycosaurs (figs. 1B and 2) the

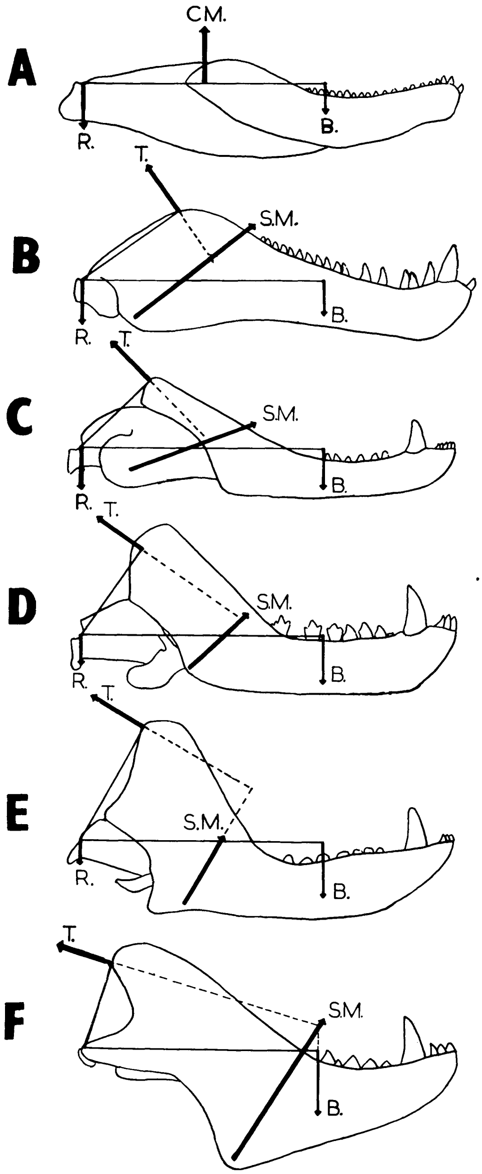


FIG. 1. External views of a series of mammal-like reptile jaws to show the progressive changes in the directions of pull and changes of position of the insertions of the temporalis, capiti-mandibularis, and superficial masseter muscles.
A, *Labidosaurus*; B, *Dimetrodon*;
C, a therocephalian; D, *Thrinaxodon*;
E, *Trirachodon*; F, *Diarthrognathus*.

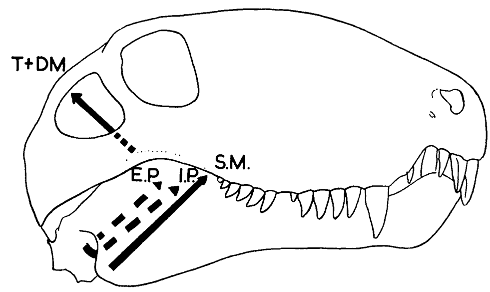


FIG. 2. Diagram to show the resultant forces of the jaw-closing muscles in *Dimetrodon*. (Lateral view of skull after Romer and Price, 1940.)

lower jaw possessed an incipient coronoid process anterior to the adductor fossa. The capiti-mandibularis mass was probably differentiated into a distinct superficial masseter (S.M.) (Parrington, 1946) that inserted on the outer surface of the reflected lamina, an external pterygoid (E.P.) that inserted in the adductor fossa (homologous with the mammalian external pterygoid), and a main component (T + D.M.) homologous with the mammalian temporalis and deep masseter. An internal pterygoid (I.P.) (anterior pterygoid of other authors)

Abbreviations for all illustrations:

ang. — angle of the dentary
ART. — articular
B. — bite force
C. — coronoid
c.boss — coronoid boss
CM. — capiti-mandibularis
con. — condyle
c.p. — coronoid process
D.M. — deep masseter
d.p. — dorsal process
E.P. — external pterygoid
i.e.p. — insertion area for external pterygoid
i.g. — internal groove
I.P. — internal pterygoid
med.r. — medial ridge
m.for. — mandibular foramen
P.ART + S.ANG. + ANG. — prearticular + surangular + angular.
Q. — quadrate
R. — downward thrust through quadrate
S.M. — superficial masseter
s.m.h — horizontal component of the superficial masseter
s.m.v. — vertical component of the superficial masseter
T. — temporalis
T + DM — muscle mass homologous with temporalis and deep masseter
t. — trough for accessory jawbones
t.j. — horizontal component of the temporalis
t.v. — vertical component of the temporalis.

probably wrapped around the ventral surface of the angular behind the attachment of the reflected lamina to the angular. The direction of the fibers of this muscle was probably the same as that of the superficial masseter. That part of the capiti-mandibularis homologous with the temporalis of later forms presumably inserted on the rudimentary coronoid process, whereas the deep masseter probably inserted in the adductor fossa. The direction of the fibers of these muscles appears to have been slightly in a posterodorsal direction so that they still formed a right angle with a line connecting their area of insertion and the glenoid. This is particularly true of those that inserted on the incipient coronoid process. Consequently, the temporalis was most efficient when the jaws were in the closed position. The anterior component of the superficial masseter appears to have balanced the posterior component of the temporalis. The enlarged temporal fossa, and greater differentiation of the capiti-mandibularis, indicate that the mass of the jaw-closing musculature in pelycosaurs was slightly greater than in the cotylosaurs.

If it is assumed that: (1) the mass and strength of the capiti-mandibularis in a cotylosaur and the temporalis and deep masseter in pelycosaurs were equal and (2) the superficial masseter represented an addition to the mass of the jaw-closing musculature in pelycosaurs, then it can be demonstrated that in pelycosaurs the vertical thrust through the quadrate (R) would have been less than in cotylosaurs despite the increase in the mass of the jaw-closing musculature. It can also be demonstrated that the vertical thrust through the upper dentition (B) would have been increased. The reason for this is that in pelycosaurs the temporalis pulled posterodorsally and not dorsally as in cotylosaurs. This can quite easily be demonstrated in a simple model of a pelycosaur and cotylosaur jaw in which elastic bands are used to simulate muscles.

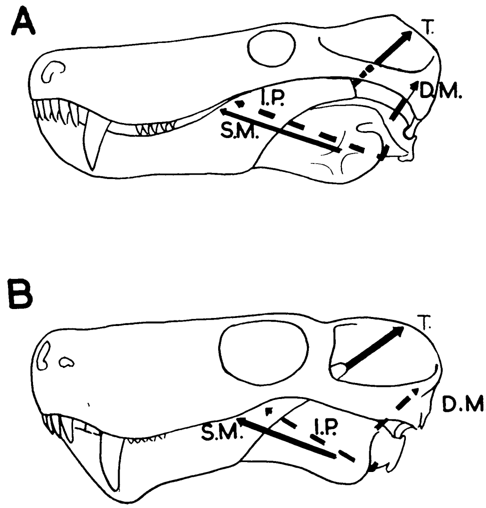
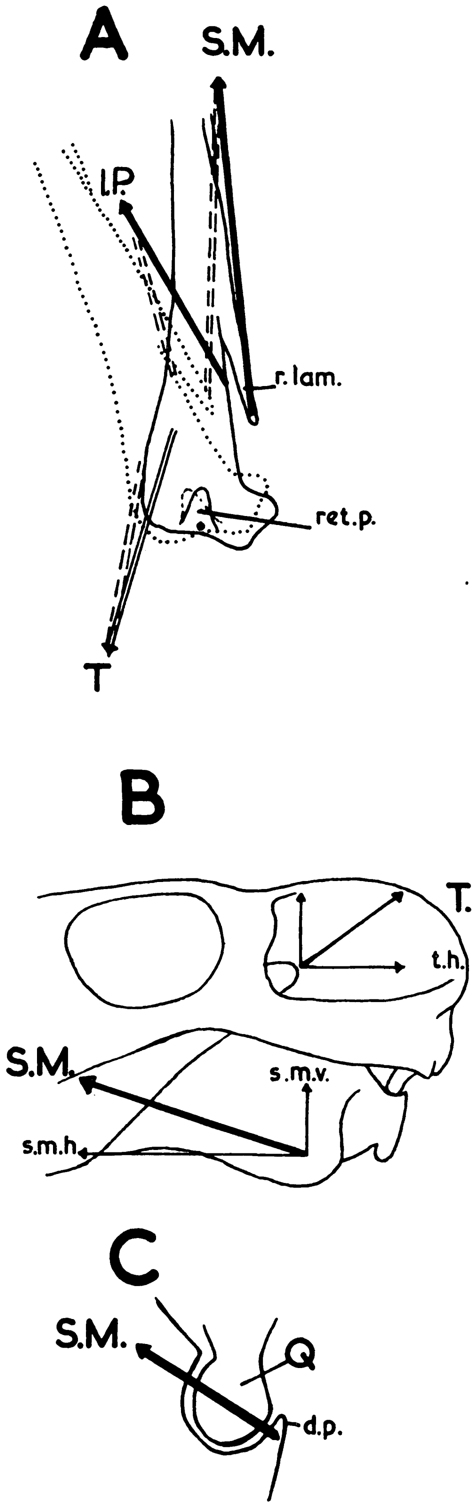


FIG. 3. A, diagram to show resultants of forces of the jaw-closing muscles in *Pristerognathoides roggeveldensis*. (Lateral view of the skull after Boonstra, 1954); B, diagram to show resultants of forces of the jaw-closing muscles of a gorgonopsian. (Lateral view of skull after Parrington, 1955.)

THEROCEPHALIA AND GORGONOPSIANS

In primitive therocephalians and fairly advanced gorgonopsians (figs. 1C, 3 and 4A, B, and C) the coronoid process was fairly well developed. The temporal opening has increased greatly in size by expanding in a posterior direction. The direction of the fibers of the temporalis muscle appears to have been closer to the horizontal than in pelycosaurs (fig. 1), but the fibers on an average still appear to have formed a right angle with a line connecting the area of insertion of this muscle on the coronoid process with the glenoid. Because of the more horizontal orientation of the fibers of the temporal muscle, the vertical thrust through the quadrate (R) was further reduced. In therocephalians and gorgonopsians the reduction in size of the accessory jaw bones, and especially the quadrate and articular, appears to be correlated with this fact.

However, the jaw joint of therocephalians, gorgonopsians, and other early therapsids was not only subjected to forces acting downward in the vertical direction (R), but also to forces acting through the jaw joint in a horizontal plane in either an anterior or posterior direction.



The horizontal components (fig. 4B, s.m.h., t.h.) of both the temporalis and superficial masseter were larger than the corresponding vertical components (s.m.v.). If these horizontal components are shown in a ventral view (fig. 4A) it can be seen that the superficial masseter is inserted on the outer surface of the lower jaw (reflected lamina, r.lam.), and the temporalis on the inner surface. When the temporalis and superficial masseter on one side of the skull contracted synchronously, therefore, they would tend to force the jaw rami anterior of the jaw joint in a medial direction. This is important only when the jaws are partly open; when closed, the transverse process of the pterygoid would prevent medial movement of the jaw ramus. Contraction of the superficial masseter alone would have pulled the jaw ramus forward, and contraction of the temporalis alone would have pulled the jaw ramus backward. These forces, either pulling the jaw backward or forward or deflecting the jaw rami, would tend to dislocate the jaw joint. However, the articular and quadrate in gorgonopsians and therocephalians were constructed to prevent dislocation. The quadrate condyle and glenoid in the articular in these forms were transversely widened. A dorsal process (d.p., fig. 4C) (Parrington, 1955) projects upward from the articular behind the lateral condyle of the quadrate and prevented the lower jaw being pulled forward when the superficial masseter contracted. The medial quadrate condyle, on the other hand, faces anteroventrally and articulates with the median part of the glenoid in the articular, which faces posterodorsally. The orientation of these articulating surfaces would have prevented the jaw ramus being forced backward when the temporalis contracted.

The jaw joint of some carnivorous mam-

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FIG. 4. Jaw-closing muscles in a gorgonopsian. A, ventral view of posterior portion of the lower jaw; B, lateral view to show horizontal and vertical components of the masseter and temporalis; C, section through the lateral portion of the jaw articulation.

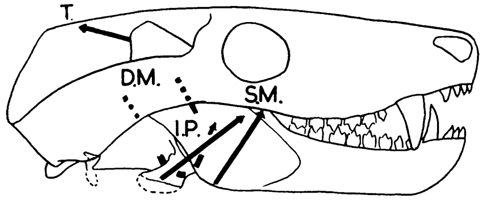

FIG. 5. *Thrinaxodon liorhinus.* Diagram to show resultant forces of jaw-closing muscles.

mals is also designed to withstand forces acting on the jaw in either an anterior or posterior direction. The adaptions in mammals are, in functional terms, almost identical to those present in gorgonopsians and therocephalians. In cynodonts, which are probably the descendants of early therocephalians, a further reduction in the size of the accessory jaw bones took place. In order to achieve this, it was necessary for these forms not only to reduce the vertical forces acting through the jaw joint but also to reduce the forces which forced the jaw either forward or backward. A reduced jaw joint would be unable to withstand the forces to which a therocephalian or gorgonopsian jaw joint was subjected.

CYNODONTS

In an early cynodont, *Thrinaxodon* (figs. 1D and 5), the dentary was, relatively, much larger than in the therocephalians. The coronoid process was greatly expanded and extended backward fairly far into the enlarged temporal opening. Its dorsal edge nearly reached the same plane as the dorsal surface of the parietal. The fibers of the temporalis were more horizontally oriented than in therocephalians. The vertical forces acting through the jaw joint (R) were, therefore, further reduced. Other important changes, however, had taken place. The deep masseter had enlarged, migrated forward, and was partly inserted on the outer surface of the expanded coronoid process. The reflected lamina of the angular was reduced in size and had migrated forward. Some of the anterior fibers of the superficial masseter had transferred their insertion from the reflected lamina onto the outer surface of the posteroventral corner of the dentary. The result was that the fibers of the superficial masseter were more vertically oriented than in ancestral forms. In therocephalians the fibers of the superficial masseter formed an angle of approximately 20° with the cranial axis. In *Thrinaxodon*, this angle had increased to about 40°. The insertion of the internal pterygoid had also moved forward and was also partially inserted on the inner surface of the posteroventral corner of the dentary. The forward migration of the insertion of the superficial masseter and internal pterygoid resulted in a slight reduction of the vertical thrust (R) acting through the quadrate, but, more importantly, it greatly increased the vertical thrust (B) acting through the posterior postcanines, i.e., the bite force when the jaws were closed was considerably increased in cynodonts. The postcanines in *Thrinaxodon* have fairly complex crowns, and it is reasonable to correlate this feature with the more sustained bite of which these animals were capable. Because the superficial masseter and internal pterygoid were more vertically oriented, they had smaller horizontal components. Consequently, neither muscle contracting alone would have forced the jaw forward to the same extent as in the therocephalians. Neither would the combined action of the temporalis and superficial masseter on one side tend to force the jaw ramus medially to the same extent as in therocephalians and gorgonopsians. Consequently, in *Thrinaxodon*, it was possible for the bones forming the jaw joint to be smaller than in therocephalians. It is interesting to note that in *Thrinaxodon* the dorsal process of the articular is represented only by a vestigial structure.

In the *Cynognathus* zone (figs. 1E and 6) and Middle Triassic cynodonts the dentary had increased further in size and the coronoid process expanded further. This was accompanied by a reduction in the size of the accessory jawbones. Most of the jaw-closing muscles had transferred their insertions onto the dentary. The fibers of the temporalis were more horizontal than in

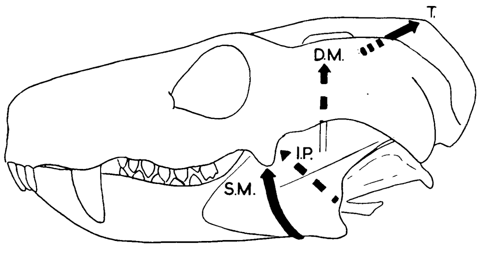

FIG. 6. *Trirachodon* sp. Diagram to show resultants of forces of jaw-closing muscles. (Lateral view of skull after Parrington, 1961.)

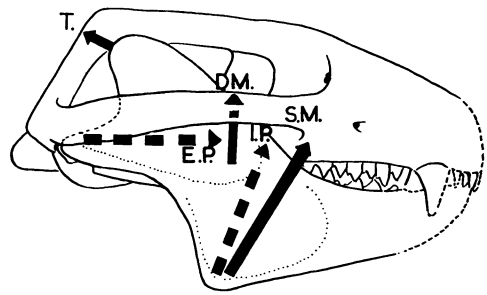

FIG. 7. *Diarthrognathus broomi.* Diagram to show resultants of forces of the jaw-closing muscles.

earlier forms, with the result that the vertical thrust through the quadrate (R) was further reduced. The dentary had a well-developed angle for the insertion of the superficial masseter and internal pterygoid. Fibers of the superficial masseter no longer inserted on the reflected lamina, and that structure is vestigial in these forms. These muscles were more vertical than in *Thrinaxodon*, and consequently the anteriorly and posteriorly directed forces to which the jaw joint was subjected were further decreased. These facts are in agreement with the further reduction in the size and strength of the jaw joint in advanced cynodonts. The power of the bite (B), on the other hand, was greatly increased. The complex crushing or cutting postcanines of these advanced cynodonts were almost certainly correlated with this fact. In therocephalians the temporalis appears to have formed a larger part of the jaw-closing musculature than in advanced cynodonts. It appears that in the evolution of the cynodonts the superficial and deep masseter and the internal pterygoid increased in mass to become the dominant jaw-closing muscles, so that the temporalis formed a smaller percentage of the jaw-closing musculature than in earlier forms.

DIARTHROGNATHUS

In the transitional form, *Diarthrognathus* (figs. 1F, 7 and 8), a rudimentary dentary condyle that articulated with the squamosal was present and the reptilian joint was extremely small. The composite condyle appears to have been weaker than in advanced cynodonts. The adaptions that were shown to decrease the forces acting on the jaw joint in earlier forms were developed a stage further. The temporalis was more horizontal than in earlier forms. The dentary possessed a deep forwardly placed angle. Consequently, the insertions of the superficial masseter and internal pterygoid were far forward, and these muscles were nearly vertically oriented.

In advanced cynodonts and *Diarthrognathus* the construction of the jaw joint was such that it could not have prevented forward migration of the jaw during the contraction of the jaw-closing muscles. It is, therefore, assumed in the sequence of jaws illustrated in fig. 1 that the muscles could adjust their strength so that the forces acting at the jaw joint did not have a horizontal component.

In *Diarthrognathus* the forces of the temporalis (T.) and the superficial masseter (S.M.) (+ internal pterygoid) would have met a downward thrust (B) through

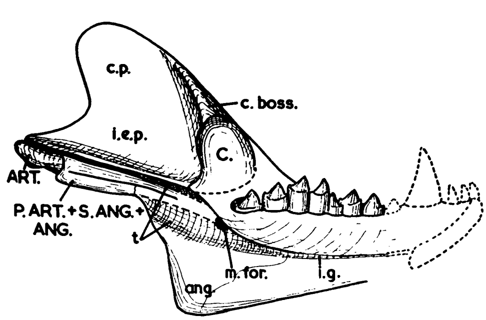

FIG. 8. *Diarthrognathus broomi.* Medial view of the lower jaw.

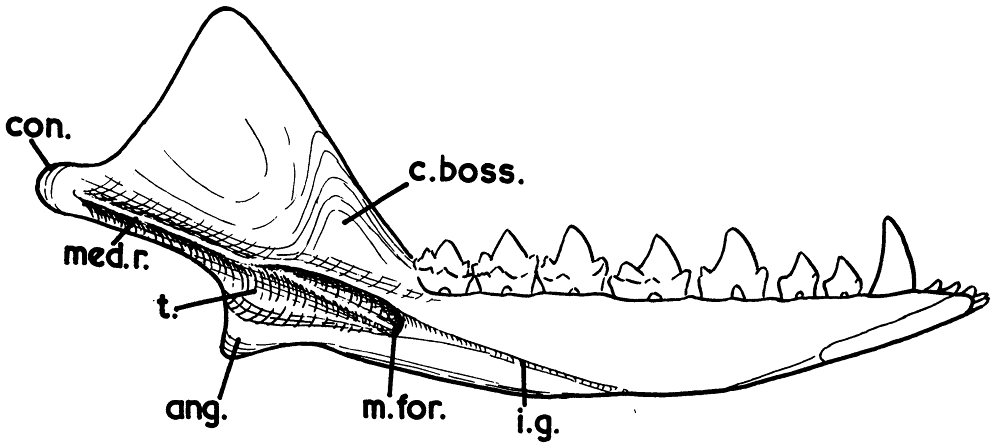

FIG. 9. *Morganucodon* sp. Medial view of dentary. (After Kermack and Mussett, 1958 and 1959.)

the posterior postcanines at a point. Since the three forces pass through a point and are in static equilibrium, there can be no force at R, otherwise its moment about the point of intersection would not be zero and the system could not be in equilibrium. Consequently, when *Diarthrognathus* was biting with its posterior postcanines, the strength of the individual muscles could have been so balanced that no vertical thrust (R) directed downward through the quadrate onto the articular was present. A similar phenomenon was described in some carnivorous mammals by Maynard Smith and Savage (1959).

In *Diarthrognathus* the superficial masseter had a very small horizontal component. Consequently, this muscle did not to any great extent tend to force the jaw forward or, when contracting synchronously with the temporalis, help to force the jaw ramus medially. Consequently, a very weak jaw joint was possible in these forms.

An interesting feature of the lower jaw of *Diarthrognathus* (fig. 8) is the anterior extent of the anterior margin of the coronoid process. It extended laterally to the posterior postcanines. This feature was also present in tritylodontids (Kühne, 1956), but is apparently unknown in Mesozoic mammals. This feature presumably enabled the insertion of the deep masseter to be as far removed as possible from the jaw joint. This would help to increase the bite across the teeth, but decrease the vertical thrust through the quadrate and squamosal to the articular and dentary.

The structure of the lower jaw of *Diarthrognathus* illustrates how it was possible to combine in one animal powerful jaw musculature and an extremely weak jaw joint. In order that this may be achieved, however, it was essential that the dentary be deep behind the dentition, have a greatly expanded coronoid process, and possess a deep, rounded, anteriorly placed angle. These features are characteristic to a greater or lesser extent of all advanced therapsids with weak jaw joints, i.e., of both carnivorous and herbivorous forms. The weaker the jaw joint, the more extreme were the adaptions to reduce the forces to which the jaw joint was subjected. The selective advantage to Triassic mammal-like reptiles of having increased jaw musculature enabling a powerful bite, and having these muscles inserted on a single bone, appears to have more than compensated for the disadvantages of having a weak jaw joint and a deep and cumbersome dentary.

MORGANUCODON

In the Rhaetic mammal *Morganucodon* (Kermack and Mussett, 1958), a double jaw articulation was still present (figs. 9

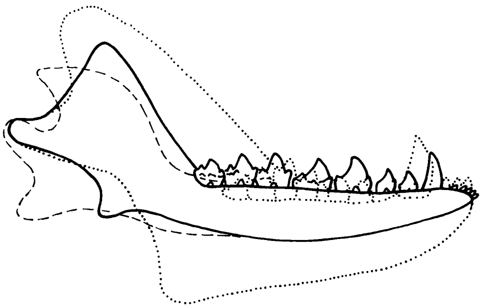

FIG. 10. Comparison of lower jaws of *Morganucodon* (———); *Diarthrognathus* (. . . .), and a pantothere (– – – – –).

and 10). The mammalian articulation was stronger than in *Diarthrognathus*, although not as strong as in later mammals. It would, therefore, be expected that the extreme adaptions necessary in *Diarthrognathus* to minimize the forces to which the jaw joint was subjected were no longer necessary in *Morganucodon*.

The lower jaw of *Morganucodon* contains a groove for the accessory jawbone similar to that present in the advanced therapsids and *Diarthrognathus*, but the general shape of the jaw is more similar to that of the jaws of Jurassic mammals than to that of an advanced therapsid such as *Oligokyphus* and transitional forms such as *Diarthrognathus*. In certain aspects the lower jaw of *Morganucodon* lies between later mammals and advanced therapsids (fig. 10). *Morganucodon* has, in comparison with *Diarthrognathus*, a long, slender dentary. The coronoid process is smaller and its anterior border does not lie lateral to the posterior postcanines. *Morganucodon* has a small angle, situated farther posteriorly than in *Diarthrognathus*. In *Morganucodon* and some of the Rhaetic and Jurissic mammals, some of the trends which characterize the evolution of the lower jaw in advanced therapsids appear to have been reversed. From early cynodonts to forms such as *Diarthrognathus*, the jaw joint progressively decreased in size while the dentary deepened and developed a deep anteriorly placed angle and an expanded coronoid process. In early mammals the newly acquired squamoso-dentary jaw joint was strengthened. The angle migrated posteriorly and decreased in depth and the width of the coronoid process was reduced.

SUMMARY

The lower jaws and jaw musculature of a series of mammal-like reptiles is briefly described and discussed. It is demonstrated how the insertion of the jaw-closing musculature in these forms gradually shifted from the accessory jawbones onto the dentary and how the component parts of the jaw musculature gradually changed their orientation in such a way that the forces to which the jaw joint was subjected during contraction of the jaw-closing muscles were progressively decreased. This made possible a reduction of the accessory jawbones and an increase in the size of the dentary until the latter bone established contact with the squamosal. The decrease in the forces to which the jaw joint was subjected was accompanied by an increase in the strength of the bite, especially in the region of the postcanine teeth. The development of "molariform" teeth in advanced therapsids appears to be correlated with this fact.

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