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FUNCTIONAL MORPHOLOGY OF THE MASTICATORY
APPARATUS OF TWO DICYNODONTS
(REPTILIA, THERAPSIDA)

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ABSTRACT

The specialized masticatory apparatus of Permo-Triassic dicynodonts (herbivorous mammal-like reptiles) is described and its function analysed by comparison of an archaic dicynodont, the pristerodont *Emydops*, with the advanced dicynodont *Lystrosaurus*. A unique feature of the dicynodont masticatory apparatus was the fact that the jaw joint consisted of two convex articulating surfaces which permitted free anteroposterior movement. Food was broken up during retraction — protraction serving merely to move the jaw forward for another retractive stroke. True pro-

palinal action did not occur. Food was comminuted by shearing; grinding or crushing was not an integral part of the masticatory cycle. In *Emydops*, cutting took place at the beak when the jaw was elevated by the vertical component of force of the external adductor muscles. Slightly later in the masticatory cycle, cutting took place at the dentary teeth as the jaw was retracted by the stronger horizontal component of force from the same muscles. The two cutting areas and the motions by which they were utilized are distinct. In *Lystrosaurus* dentary teeth are lacking and the cutting area at the front of the jaws is expanded. Motion of the lower beak consisted of a combination of elevation and retraction by the powerful horizontal component of the muscles. During much of the Upper Permian and Lower Triassic, when dicynodonts were the dominant tetrapod herbivores, their peculiar masticatory apparatus enabled them to invade an environment apparently barred to conventional herbivores. The line leading to *Lystrosaurus* probably originated from an *Emydops*-like form, the main trend of evolution being toward increasingly effective utilization of the horizontal component of force exerted by the external adductors. However, the pristerodonts persisted with little change during most of the interval in which this evolution took place. It appears that the archaic jaw mechanism of pristerodonts was adapted in some way to a persistent environment which was different from the environment that favored the *Lystrosaurus* type of specialization.

INTRODUCTION

The infra-order Dicynodontia (*sensu* Romer, 1956) is a group of highly specialized, herbivorous, therapsid reptiles that makes its first appearance in the fossil record of the late Permian *Tapinocephalus* zone of the Beaufort Series of South Africa. Dicynodonts are the most abundant fossils in the succeeding late Permian *Endothiodon* and *Kistecephalus* zones, in the early Triassic *Lystrosaurus* zone, and in the time equivalents of these beds in East Africa, China, India and Europe. In the early Triassic *Cynognathus* zone of the Beaufort Series, early in the late Triassic Er-May-Ying of China and the middle Triassic deposits of East Africa and South America, the fossil fauna of herbivorous tetrapods is more varied because of the cynodont and rhynchosaur

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radiations characteristic of that time, but dicynodonts continue to form a significant part of the total. In the latest Triassic (e.g., of North America), the dicynodonts dwindle rapidly until they are represented by only a few large forms. They are not known from the Jurassic.

Dicynodonts of the *Tapinocephalus* zone were relatively small forms; the large herbivores of the fauna were members of either the Dinocephalia or Parieasauria. At the end of *Tapinocephalus* zone times, dinocephalians became extinct; parieasaurs declined in numbers but survived through the late Permian. The dicynodonts, on the other hand, expanded rapidly in numbers and variety to become the dominant tetrapod herbivores during the time span of the *Endothiodon*, *Kistecephalus* and *Lystrosaurus* zones.

The success of the dicynodonts during the late Permian and early Triassic appears to have been due in large part to their highly specialized masticatory apparatus. Evidently this specialization enabled them to utilize plant material more effectively than the earlier reptilian herbivores; as a result they were able to invade environments barred to reptiles with a more conservative jaw mechanism. A similar apparatus has not evolved in any other vertebrate group, although chelonian jaw structure is in some ways reminiscent of that of dicynodonts.

The abundance and diversity of the therapsid fossil record of the late Permian suggests that it represents a comprehensive sample of the original fauna. As such, it provides a unique opportunity for the study of an integrated terrestrial tetrapod fauna of sub-mammalian level and great age. In various members of this fauna, especially those which were insectivorous and carnivorous, many of the characteristic features of mammals made their first appearance during the late Permian. As successful herbivores, the dicynodonts must have comprised a vital part of the food chain of predaceous therapsids; the study of them is therefore important because it may throw light on the environment in which some mammalian characters arose.

Most of the extensive literature on dicynodonts concerns taxonomy (Haughton and Brink, 1954), which is, of course, prerequisite to progress in ecologic and phylogenetic studies. Unfortunately, however, the taxonomy of the group is confused, chiefly because most current classifications are based upon isolated fea-

tures whose biological meaning is poorly understood. Very little attempt has been made to interpret the total cranial structure in functional terms.

An exception is the monumental contribution of Watson (1948), in which it is demonstrated that the peculiar articulation of the jaw in dicynodonts enabled the mandible to move freely backwards and forwards through a long distance, and permitted variation in the angle at which the lower jaw approaches the upper jaw. Watson envisaged a propalinal movement — the lower jaw moving back and forth while pressed firmly against the palate. He concluded that in typical dicynodonts there was a horny beak with a sharp, cutting periphery and roughened crushing surfaces on the palate and dorsum of the lower jaw, which served to cut, crush and grind vegetable food. His conclusions have been accepted by succeeding workers in the field. Camp (1956), Camp and Welles (1956), Cox (1959, 1964, 1965) and Ewer (1961) have also provided valuable morphological and functional data on the cranial anatomy of dicynodonts.

Although the basic structure of the masticatory apparatus is uniform throughout the Dicynodontia, the group varies in body size from forms no larger than a rat to forms as large as an ox. The shape of the skull varies enormously, from narrow and deep to broad and shallow, and is not closely correlated with size. Detailed studies of all major types of dicynodonts must be undertaken in order to understand: 1) the adaptive significance of the various types of skulls; 2) taxonomy and evolution of the group; and 3) dicynodont ecology, including the factors contributing to the success of the group during most of the late Permian. Sufficient material is now at hand to initiate such a long-term study.

The present paper consists of a description and functional analysis of the jaw mechanism of an archaic dicynodont, *Emydops*, and an advanced dicynodont, *Lystrosaurus*. In part, these particular genera were chosen for study because of the availability of undistorted material that could be prepared in acid. In the prepared skulls of these two genera the types of probable jaw movements could be determined in far greater detail than had previously been possible. The quality of the material also permitted reliable analysis of the mechanics of the jaw joint, reconstruction of the jaw muscles, and interpretation of the overall shape of the skull

in functional terms. This program has been carried out with full recognition of the fact that jaw muscles and movements in any animal are far more complex than can be reconstructed from fossil remains, particularly, as in the case of the dicynodonts, where there are no living forms similar to the animals in question.

Because of the rarity of undistorted material and the refractory nature of most of the Beaufort matrix, we believe that few of the major forms can be studied in comparable detail. The present work, therefore, is intended to serve as a basis for the interpretation of function in other kinds of dicynodonts. Several major groups are currently under independent study from the point of view of cranial morphology and taxonomy, and it is felt that more extensive consideration of the Dicynodontia as a whole would be premature at this time.

THE MASTICATORY APPARATUS IN THE PRISTERODONT *EMYDOPS*

The following description is mainly based upon an uncrushed specimen of a *Kistecephalus* zone pristerodont *Emydops* in the Bernard Price Institute, Johannesburg (BPI 401), prepared in acetic acid so that the lower jaw was completely freed from the skull (Fig. 1).

CRANIAL ANATOMY

The cranial anatomy of *Emydops* is similar to that of *Synostocephalus*, described in detail by Watson (1948). The presence of postcanine teeth in these forms is a primitive feature, but in other respects they have all the characters that can be defined as distinctively dicynodont. Except for postcanine teeth and the specific function deduced from them, anatomical and functional statements about *Emydops* can be applied to dicynodonts in general.

The temporal region is large in proportion to the face, and provides attachment for the laterodorsal trigeminal musculature of enormous bulk. In addition to the large size of the temporal vacuities as seen in dorsal view, the ventrolateral region of the cheek is deeply excavated (Fig. 1C). From the posterior root of the zygoma a large process of the squamosal (sq.) slants downwards and slightly forward, bearing the quadratojugal (q.j.) and the reduced quadrate (q.) on its distal end. This process was

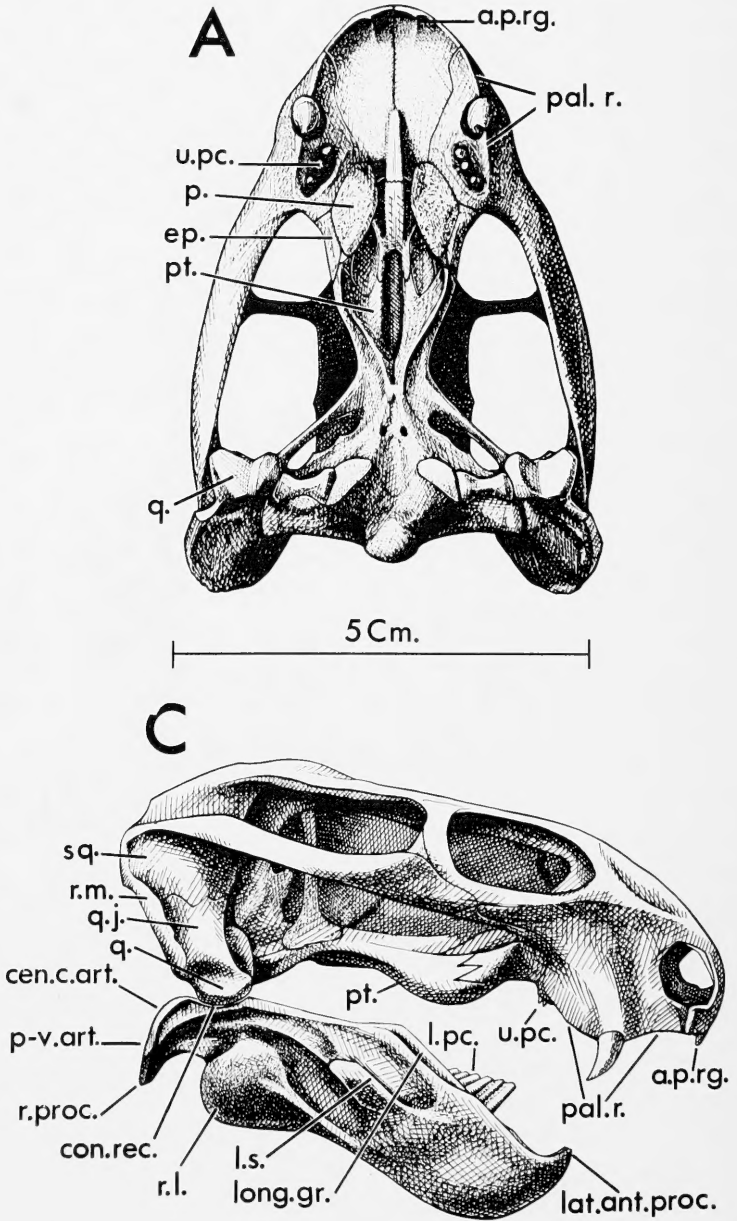
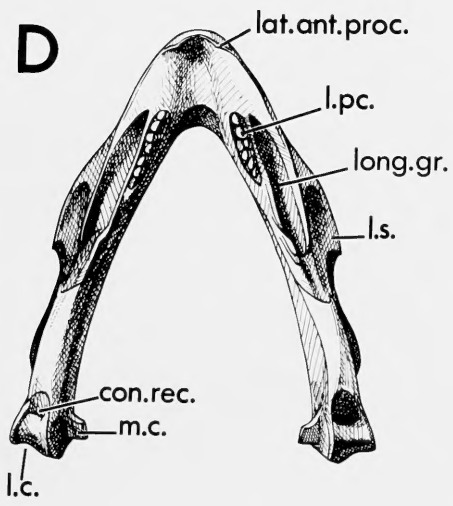
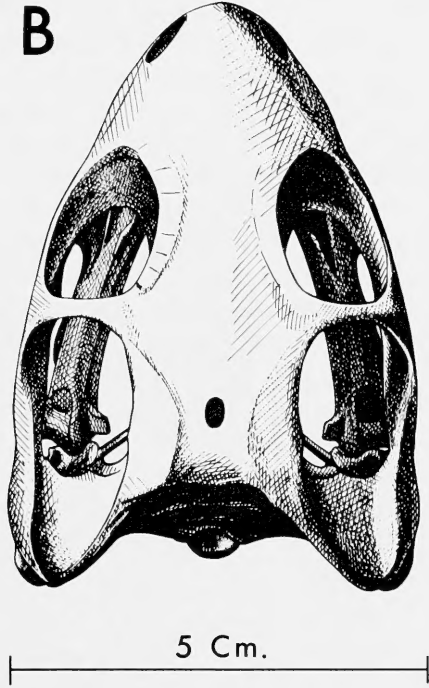


FIG. 1. *Emydops* sp. A, ventral view of the skull, B, dorsal, and C,



lateral; D, dorsal view of the mandible. See Key to Abbreviations, p. 49.

termed the otic pedicle by Owen (1876), presumably because of its resemblance to the large vertical quadrate which supports the tympanum in lizards. However, in dicynodonts the process does not bear the same functional relationship to the middle ear and is better termed the suspensorium (Watson and Romer, 1956). The posterior margin of the suspensorium is reflected sharply laterally and projects to the side (r.m.) beyond the lateral margin of the quadrate. The reflected margin is well developed in all dicynodonts, although in some (e.g., *Daptocephalus*), reflection is restricted to the lower half of the suspensorium.

The basicranial region is tightly knit. No transverse processes or flanges such as those characteristic of the theriodonts and most other reptiles are developed on the pterygoids (pt.). Instead, the palatine rami of the pterygoids pass forward as blade-like structures. Their anterior ends are sutured to the back of the palate between the palatine (p.) and the ectopterygoid (ep.) bones (Fig. 1A).

A secondary palate of characteristically dicynodontian structure, consisting of a broad, flat, horizontal plate, is formed anteriorly by the premaxillae and the maxillae. It is continued posteriorly by the palatines, which dip gently downward to the rear. The profile of the roof of the palate is shown as a dotted line (r.p.) in Figure 5C and D. Around the anterior and lateral margins of the secondary palate the premaxillae and maxillae are produced downward as a distinct outer rim (Fig. 1A: pal.r.). The rim is best developed in the region of the canines. In *Emydops* it is less prominent than in more advanced dicynodonts. Anteriorly, the rim is continued slightly further downwards, forming a tip to the upper beak. Two faint ridges arise from the tip of the beak and run backward, parallel to the midline, on the ventral surface of the palate. These are designated the anterior palatal ridges (Fig. 1A: a.p.rg.), and are visible below the margin of the palate in lateral aspect (Fig. 1C).

Three functional postcanine teeth are present in the upper jaw (u.pc.); in cross-section, their crowns are round to slightly widened transversely and are unserrated. They are arranged in a straight line parallel to the mandibular teeth. A narrow space separates the outer faces of the maxillary teeth from the palatal

rim behind the canines. Only the tips of the two posterior teeth are visible below the palatal rim in lateral aspect (Fig. 1C).

There are seven functional teeth in the lower jaw (l.pc.). The crowns are pear-shaped in cross-section, the wide, blunt anterior edges contrasting with the sharp, strongly serrated posterior edges. This shape indicates that the teeth were effective in cutting only as the jaw moved backwards. In *Endothiodon* (Cox, 1964), the teeth evidently functioned in the same way—sharp, serrated margins being developed on the back of the lower teeth and on the front of the upper teeth.

The lower teeth of *Emydops* are supported on the medial edge of the dorsum of the dentary; they are pressed closely together to form a composite blade with a narrow, serrated cutting edge, oriented parallel with the long axis of the jaw ramus. The anterior teeth are markedly higher than the posterior teeth, so that the profile of the tooth row corresponds to the curved ventral surface of the palatine. As a consequence, all the teeth could be opposed to the palate simultaneously. Mandibular teeth were apparently replaced frequently (Hopson, 1964). Replacement teeth, which are clearly visible in the acid-prepared specimen, erupted closely applied to the medial surface of the functional teeth, maintaining the blade-like configuration of the tooth row.

Lateral to the teeth, the dorsal surface of the dentary is broad and bears a wide longitudinal groove (long.gr.). The groove commences lateral to the anterior teeth and continues in a posterolateral direction to terminate near the posterior corner of the dentary well behind the mandibular teeth.

The dentary (Fig. 1C & D) is extremely massive at the symphyseal region and is stouter than the relatively slender and lightly built postdentary bones. In *Emydops* the symphyseal region is shorter than in more advanced dicynodonts. On either side of the midline the anterodorsal tips of the dentaries support two short but sharp processes (lat.ant.proc.) directed dorsally. They clearly match the anterior palatal ridges of the premaxilla.

In Figures 2A and 5C the jaws are shown closed and protracted. Their bony tips are still separated by a considerable distance and cannot be brought together without dislocating the joint. The dorsal and anterior surface of the dentary symphysis, the palatal and facial surfaces of the premaxilla and maxilla, and the

palatal surface of the palatines are perforated by numerous foramina. Because of the similar appearance of these bones to the horn-bearing bones of birds and turtles, they are generally assumed to have supported a horny beak. In *Chelonia*, the shape of the underlying bone reflects the shape of the horny beak; a sharp process of bone is usually covered by a sharp and long process of horn. Similarly, the sharp processes on the tips of the dentaries and premaxillae of *Emydops* probably supported projections of horn (Fig. 2A: h.b.) that were long enough to overlap one another. In the upper jaw this projection was probably continued around the margin of the palate as a horny rim, covering the bony rim of the palate (pal.r.). In contrast, the dorsal surface of the dentary, between the anterior process of the mandible and the teeth, does not form a sharp edge, and therefore presumably did not support an elevated lamina of horn. The outline of the symphysis in dorsal view matches the outline of the palate, so that when the jaw was closed in a protracted position the horny covering of the dorsal symphyseal region would have fitted closely inside the external rim of the palate (Fig. 4D).

This relationship provided the more anterior of two zones of contact between the lower and upper jaws, and was effective only in extreme protraction. The more posterior contact took place between the apices of the mandibular teeth and the ventral surface of the palate medial to the upper teeth. Watson (1948) has suggested that the upper teeth bit against a horny pad contained in the longitudinal groove on the dorsal surface of the dentary. However, the upper teeth are much shorter than the lower. When the jaw was protracted the upper teeth were directed towards the anterior end of the longitudinal groove, but they were too short to have reached the dorsal surface of the dentary, even if it had been built up by a horny pad. Retraction moves the groove further away from any functional relationship to the upper teeth. The pattern of nutrient foramina in acid-prepared specimens indicates that there was no horn covering the groove. These three features strongly indicate that the upper teeth had no functional relationship with any part of the lower jaw such as the lower teeth had with the palate. Because of this and other reasons discussed below we feel that the longitudinal groove served as an insertion for the medial part of the dorsolateral trigeminal musculature.

On the outer surface of the dentary a short, massive lateral shelf is developed behind the level of the anterior mandibular teeth (Fig. 1C & D: l.s.) The shelf increases gradually in width in a posterior direction (Fig. 1D) and terminates abruptly at a point below the posterior end of the longitudinal groove of the dentary. The upper surface of the shelf grades smoothly into the lateral surface of the dentary. In many specimens the lateral face of the dentary bears a broad, flat muscle scar just above the lateral shelf. This scar and the dorsal surface of the shelf mark the insertion of the lateral part of the dorsolateral trigeminal musculature.

The reflected lamina of the angular bone (Fig. 1C: r.l.) is distinctive. It is large and fan-shaped in *Emydops* as in other small dicynodonts. Posteriorly and ventrally it consists of a broad, thin, unsupported sheet that terminates in a long, free border. In many dicynodonts the sheet exhibits two or three coarse folds that converge anteriorly toward a marginal thickening on the body of the angular. No thickening or ribbing of the unsupported posterior portion was observed in any of several specimens of *Emydops* examined.

The condylar surface of the lower jaw is divided into a broad, long lateral portion (Fig. 1D: l.c.) and a narrow medial portion (m.c.). The lateral condylar surface of the articular consists of three distinct parts, best seen in lateral view (Fig. 1C & 3B): 1) an anterior concave portion here designated the condylar recess (con.rec.); 2) a central convex portion which describes the arc of a circle (cen. c. art.); and 3) a posteroventral flat portion (p-v. art.) whose surface is tangential to the circle described by the central portion. The posteroventral articular surface is continued downward onto the back of the retroarticular process (r.proc). The medial condylar surface is much shorter than the lateral condylar surface but it also describes the arc of a circle.

The quadrate's contribution to the joint consists of a relatively simple condyle. A broad, shallow groove on its ventral surface divides the condylar surface into lateral and medial portions (Fig. 1A) that correspond to the lateral and medial condylar surfaces of the articular. The articular surface of the quadrate condyle is much shorter than the lateral condylar surface of the articular, indicating that the lower jaw was capable of extensive anteroposterior movement.

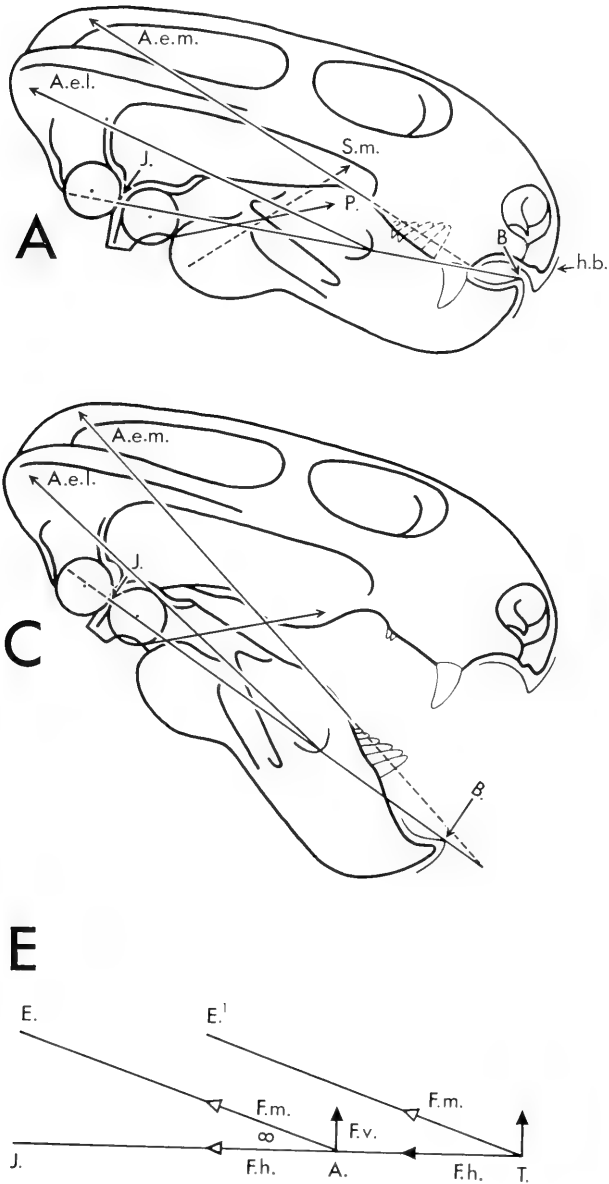
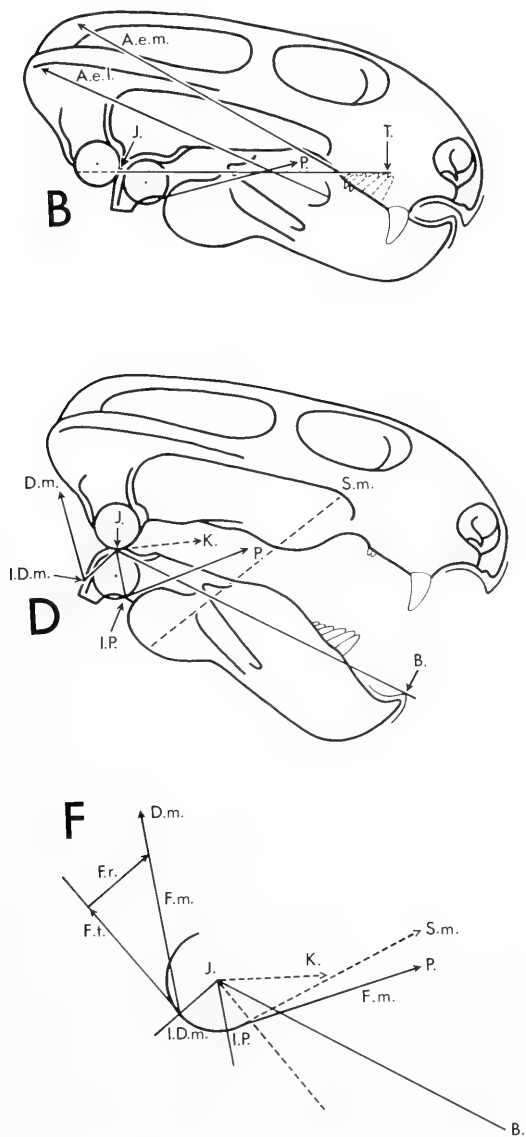


FIG. 2. *Emydops* sp. Traction lines of the main masticatory muscles and their relationship to the jaw axis at selected positions of the masticatory cycle. A, beak bite; B, commencement of retraction; C, beginning of eleva-



tion; D, depression and protraction; E, analysis of the traction line of a single muscle; F, analysis of the components of force of the depressor mandibulae and the pterygoideus.

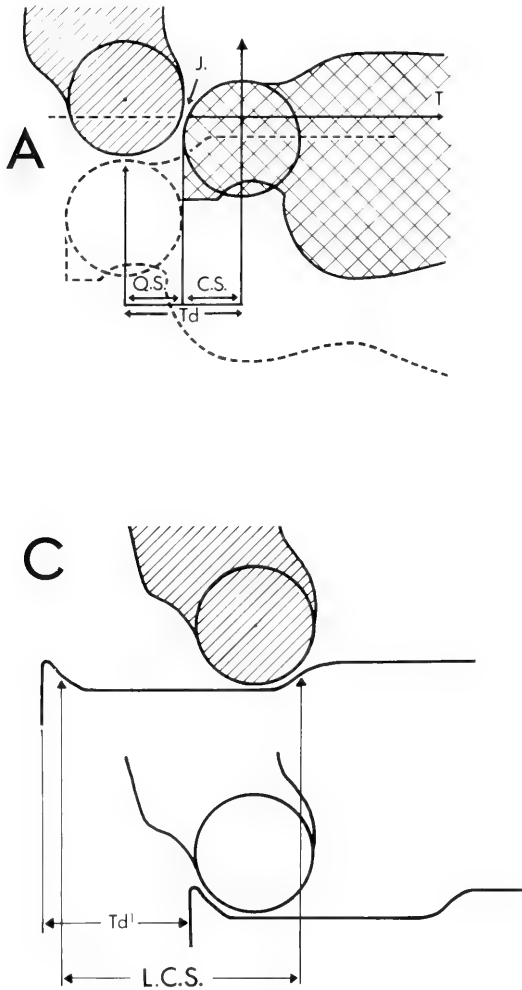
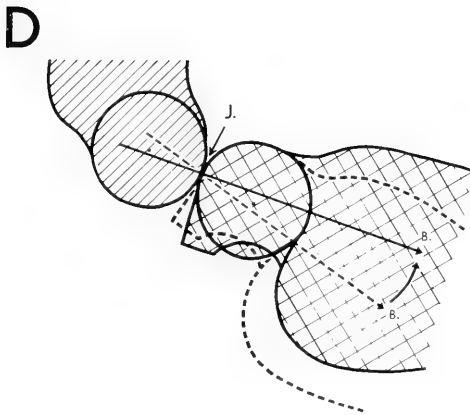
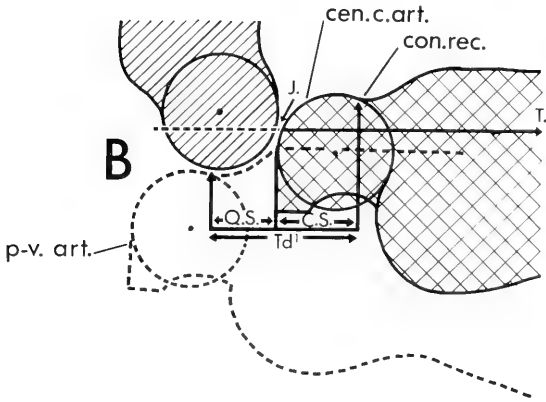


FIG. 3. *Emydops* sp. Analysis of the jaw joint. A, retraction of lower jaw from fully protracted (solid lines, cross-hatched) to partial retracted position (dotted lines) in order to illustrate that the total movement T_d does not exceed the combined radii of the arcs of the quadrates and articular condyles. B, retraction of lower jaw from fully protracted to fully retracted position in order to illustrate that the greatest amount of movement pos-



sible (Td^1) does not greatly exceed the sum of the radii of the two arcs. C, hypothetical jaw joint, designed to withstand powerful vertical pressure during protraction. D, elevation of lower jaw (dotted lines to solid cross-hatched) to illustrate the buttressing action of the posteroventral portion of the condylar surface when the lower jaw is depressed.

The articular surface of the lateral quadrate condyle describes the arc of a circle of nearly the same radius as that described by the convex central portion of the lateral condylar surface of the articular (Fig. 3A). Because both of these surfaces are convex they are not congruent with each other. The incongruent surfaces are in contact with each other during protraction of the lower jaw, at which time the joint was unstable (Fig. 2A & B). The anterior condylar recess is the only part of the surface of the articular with which the quadrate condyle is congruent. These surfaces come into contact at full retraction of the lower jaw (Fig. 5D and Fig. 3B; broken lines), at which time the joint is stable.

The motion imparted and force exerted by the masticatory muscles are described by reference to the axis of the mandibular ramus, which is here defined by posterior and anterior points of static resistance; this line runs through the major insertions of the trigeminal muscles. In reality, the points of static resistance vary continuously throughout any cycle of jaw action because of the shapes of the joint and the occlusal surfaces at the front of the jaws. An infinite number of lines can therefore be drawn. However, as is demonstrated in the following pages, the most significantly different points are related to the bite at the front of the jaws, and differ according to whether the bite under consideration takes place at the beak or between teeth and palate. For the sake of simplicity, the posterior point defining the axis of the mandibular ramus is considered as a single contact between upper and lower articular surfaces; the anterior point may be the contact between the mandibular teeth and palate (Fig. 2B: JT), or between the tips of the lower and upper beaks (Fig. 2A: JB). Thus, only two lines need be considered; either one of the lines illustrates the radius of rotation around point J. (elevation and depression) and provides a diagram of the jaw as a third-class lever.

In Figure 3B the jaw joint is shown in a protracted position (solid line) and in a retracted position (broken line); the mandible is elevated in both cases. When the jaw was elevated in full protraction, the center of arc of the articular condyle lay slightly below that of the quadrate condyle and the posterior extension of the line JT passed between the centers. A horizontal force exerted to the rear along line JT would have driven the articular condyle

down the face of the quadrate condyle, which acted as an inclined plane. The downward component of motion ceased when the articular reached the lowest point on the quadrate; the articular slid backwards until the condylar recess came to rest against the quadrate condyle and helped preclude further retraction. This motion was principally translative because it involves the sliding of the articular over the quadrate, in contrast to rotation at the joint.

When the jaws were widely opened in a protracted position (Figs. 2C and 3D: dotted lines), the axis of the jaw ramus (JB) would have passed below the center of arc of the condylar surface of the articular and above the center of arc of the quadrate condyle. The horizontal component of force of the external adductor muscles would have been directed posteriorly along line JB. Consequently, if there had been no posteroventral extension of the articular surface (Fig. 1C; p-v. art.), contraction of the muscles would have tended to force the jaw backwards above the quadrate rather than below it. However, the posteroventral portion of the articular surface is tangential to the convex portion, and normal to line JB. It therefore acted as a stop, resisting posterior motion along JB when the jaw was depressed and protracted. In this position, the horizontal component of the external adductors only served to press the back of the articular against the quadrate, which would help to stabilize the joint. The depressor mandibulae (Fig 5A) would also serve to press the articular against the quadrate and would have contributed to stabilization. Because the jaw could not be retracted when it was fully depressed, contraction of the external adductors could only serve to elevate the jaw, with the joint serving as a simple hinge. However, as the jaw was elevated, its axis would change orientation until it passed above the center of arc of the articular condyle and below the center of: solid lines arc of the quadrate condyle (Fig. 3D). This would result in retraction and would prevent an effective bite at the tips of the beak. This point is elaborated further below in connection with muscle forces at specific positions of the jaw.

The advantages of the dicynodont jaw in terms of fore-and-aft motion are illustrated by comparison of Figures 3A and B. In Fig. 3A the anteroposterior movement (Td) of the lower jaw is equal to the sum of the radii of the arcs of the articular (C.S.) and the quadrate (Q.S.) condyles: $Td = C.S. + Q.S.$ The posterior posi-

tion shown in Fig. 3A (broken lines) would leave the lower jaw in an unstable position, and posterior movement would certainly have had to continue until the quadrate condyle rested against the condylar recess (Fig. 3B). Therefore, the maximum anteroposterior distance of movement (Td^1 in Fig. 3B) was, in fact, slightly greater than the combined radii of the arcs of the articular surfaces. The types of jaw joint illustrated in Figs. 3A and 3B could not have been subjected to major vertical forces when in protracted (solid line) or semi-protracted position. If the joint were subjected to substantial vertical forces during mastication, it would have had to be constructed to withstand such forces. A hypothetical joint capable of withstanding vertical forces in both the protracted and retracted position is illustrated in Fig. 3C. If the same amount of anterior-posterior travel (Td^1) shown in Fig. 3B had been possible in the joint shown in Fig. 3C, the articular surface (L.C.S.) would be nearly twice as long as the anteroposterior movement (Td^1) of which the jaw was capable. This would result in a long piston of bone extending into the neck musculature. By utilizing two convex articular surfaces, long fore-and-aft travel was attained without the necessity of such an ungainly arrangement. The shape of the jaw joint of dicynodonts was also closely correlated with modifications of proportions and orientation of the jaw musculature.

JAW MUSCULATURE

The elements of dicynodont jaw function deduced from anatomical features described in preceding pages are summarized as follows:

1. The jaw must have been capable of extended fore-and-aft motion because the lower articular surface of the joint is much longer than the upper.
2. The "power stroke" of mastication was retraction rather than protraction because
 - a. The posterior margins of the lower teeth were sharp and serrate, whereas the anterior surfaces were blunt;
 - b. Upward force would be exerted at the joint in any power stroke; in a protracted or semi-protracted position the joint was subject to dislocation because of this force.

In a retractive power stroke the great horizontal component of force tended to press the joint surfaces together and thereby to resist dislocation. A protractive power stroke would have tended to pull the joint surfaces apart and to increase instability of the joint.

3. A bite between the tips of the horny beak was only possible when the lower jaw was fully protracted.

The trigeminal musculature which serves these functional requirements is restored in Figure 4. Morphology of the dicynodont jaw musculature conforms to a reptilian pattern and bears a striking resemblance to comparable muscles of a living iguanid lizard such as *Ctenosaura* (Oelrich, 1956) or *Crotaphytus*. Therefore, the terminology of Brock (1938) is appropriate. Brock divided the adductor externus group in lizards into adductor externus lateralis and medialis¹. The same division can be recognized in the dicynodonts.

The adductor externus lateralis (Fig. 4A: A.e.l.) probably arose from the concave lateral face of the suspensorium and from the ventral surface of the zygoma, with the origin extending forward as far as the postorbital bar. The muscle fibers slanted obliquely forward and downward to insert on the dorsum of the lateral shelf of the dentary and into a concave area above the shelf. The adductor externus medialis (Fig. 4B: A.e.m.) probably filled the temporal fossa, originating from its medial and posterior margins (postorbital and dorsum of squamosal bones, respectively). The muscle fibers ran obliquely forward and downward, parallel to those of the lateral external adductor, and inserted into the longitudinal groove on the dorsal surface of the dentary. The insertion may have extended onto the dorsum of the surangular immediately behind the dentary, and a short distance down the medial side of the mandible. As demonstrated in the following section, these two muscles are the prime movers in elevation and retraction of the lower jaw.

The corner of the mouth behind the tusk or caniniform process may have been delimited by a membrane (*Mundplatt*) similar to that of lizards (Oelrich, 1956). In view of the great range of fore-and-aft movement of which the jaw was capable, this mem-

¹These are the muscles called *capiti-mandibularis superficialis lateralis* and *medialis* by Adams (1919).

brane (Fig. 4A: mp.), if present, must have been large. Its anterior limit would have coincided with the posterior limit of the horny beak. Its posterior corner would have been placed near the front margin of the adductor externus medialis, but the exact position is not certain. The arrangement is similar to that found in many lizards. As restored, the *Mundplatt* is functionally adequate for any gape of which a dicynodont was capable.

The *Mundplatt* of lizards is kept taut and out of the way of the jaw by the levator angularis oris, a very thin, flat, superficial muscle arising from the infraorbital bar. If the dicynodonts had a large *Mundplatt*, as suggested above, it is probable that they also had a large levator angularis oris (Fig. 4A: L.a.o.). Restoration of the posterior margin of the muscle is difficult because its attachments are generally indistinct. However, in lizards it covers most of the lateral surface of the adductor externus lateralis, and there is no reason to suppose that dicynodonts did not have a similar arrangement.

Of the internal adductor group, only the evidence of the presence of the adductor internus pterygoideus of Brock (pterygoideus anterior of Adams) can be readily identified in dicynodonts. It arose from the lateral surface of the pterygoid, the origin perhaps extending forward onto the ectopterygoid as described by Watson (1948). The fibers were directed posteriorly and ventrally, passing around the ventral margin of the angular to insert on the lateral rim of the articular as in sphenacodont pelycosaur (Romer and Price, 1940). This muscle is simply referred to as the pterygoideus in the present study and is a prime mover of protraction (Fig. 4C and D: P.).

As noted by most previous workers, a depressor mandibulae (Fig. 4C; D.m.) occupied the normal reptilian position behind the jaw joint, originating from the back of the squamosal and inserting near the distal end of the down-turned retroarticular process. This muscle served to depress the jaw.

In addition to these readily recognizable muscles, an adductor internus pseudotemporalis of Brock (Fig. 4C and D: Ps.) (capiti-mandibularis profundus of Adams), referred to below as the pseudotemporalis, probably occupied the space between pterygoideus and adductor externus medialis. None of the other attachments of the pseudotemporalis can be defined with confidence.

As in lizards, the fibers of the pseudotemporal portion of the adductor internus were probably mingled with those of the adductor externus medialis in the dorsal part of the origin and the anterior part of the insertion of the pseudotemporalis. The fibers of the pseudotemporalis mingled with fibers of the pterygoideus where the two muscles adjoined anteriorly. The function of the pseudotemporalis must have been more complex or, at any rate, more difficult to analyze than that of the other jaw muscles because of its transverse orientation. The anterodorsal fibers of the pseudotemporalis running parallel to those of the adductor externus medialis probably contributed to elevation and retraction of the jaw. Those fibers which inserted on the articular undoubtedly aided protraction. The remainder—short fibers running from pterygoid and epityergoid to mandible—probably helped stabilize the back of the jaw during both protraction and retraction. Because of the vagueness of its attachments, little more can be said of either structure or function of the pseudotemporalis.

A single slip of the adductor internus musculature (Fig. 4D: P.p.) probably inserted on the front of the medial condyle of the articular. Parrington (1955) recognized a similar muscle in the gorgonopsians.

The restoration outlined above is similar to that proposed by Watson (1948), except that he designated the subdivisions of the external adductors as "temporalis" and "masseter." We prefer not to use these terms because in dicynodonts the two muscles in question are not strictly homologous with the mammalian temporalis and masseter. Parrington (1955) postulated a masseter (superficial) in gorgonopsians, which originated on the ventral surface of the infraorbital bar and extended obliquely backwards to insert on the lateral surface of the reflected lamina of the angular (Fig. 1: r.l.). Cox (1959) and Ewer (1961) proposed a similar muscle in dicynodonts. Cox suggested that the passage of the superficial masseter behind the lateral shelf accounts for the abruptness of the posterior termination in the latter. However, the abruptness of termination of the shelf could also reflect the need to have limited the insertion of the lateral adductor muscle to the anterior part of the mandible, a basic feature of the mechanical organization of the dicynodont jaw (see below).

In cynodonts a scar or process on the inferior margin of the

infraorbital bar is believed to indicate the presence of a superficial masseter, because in most mammals a similar scar in the same region marks the origin of this muscle. Cox (1959) interpreted a distinct process below the orbit in *Endothiodon* and closely related genera as serving for the origin of a superficial masseter. No indication of such a process or a scar on the ventral surface of the infraorbital bar was found in any dicynodont studied by us. However, the anterior termination of the adductor externus lateralis does extend forward to an area below the postorbital bar in all dicynodonts including *Emydops*, so that muscle scars in this region need not indicate the presence of a superficial masseter. *Aulacephalodon* has a large boss at about the middle of the zygomatic arch. It has a heavily sculptured external surface which probably lay just below the skin. Cox has also interpreted this as an origin for a superficial masseter, but the ventral surface of this boss lies well behind the postorbital bar and undoubtedly formed part of the origin of the adductor externus lateralis.

The reflected lamina in dicynodonts has a limited area of attachment to the angular, from which it spreads out broadly to the rear to form a thin, unsupported sheet of bone. The surface is slightly folded, the folds radiating from the attachment to the angular. Although these gentle folds would strengthen the lamina to a degree, they are not oriented so as to resist stress applied in an anterodorsal direction, such as would obtain if a powerful superficial masseter were inserted on the lamina. Thus the areas postulated as insertion and origin of a superficial masseter muscle do not provide convincing argument for the presence of this muscle in the dicynodonts. As is demonstrated in the following section, the postulate of a strong muscle situated in the position of a superficial masseter cannot be integrated into the overall pattern of jaw action of this group.

The objections raised here to the suggested presence of a superficial masseter are by no means conclusive, but they suggest that such a muscle either was not present in dicynodonts or was insignificant in size. This conclusion is also supported by recent work (unpublished manuscript, H. Barghusen, 1966) on the evolution of therapsid and mammalian jaw musculature. Barghusen has shown that a muscle originating on the ventral margin of the infraorbital bar and inserting on the outer surface of the reflected

lamina, homologous with the mammalian superficial masseter, was almost certainly not present in primitive therapsids, i.e., therocephalians (including whatsiids, scaloposaurids, and bauriamorphs), gorgonopsians, and dinocephalians. It is likely that a true superficial masseter arose for the first time in Triassic cynodonts.²

Pelycosaurs and primitive therapsids (Dinocephalia, Gorgonopsia, Therocephalia and Bauriamorpha) exhibit a generalized reptilian pattern of musculature in which the pterygoideus mass was probably larger than the adductor externus mass. The pterygoideus arose from the back of a massive transverse process of the pterygoid and from the body of the quadrate ramus of that bone, and inserted on the medial side of the mandible. In sphenacodont pelycosaurs and all later therapsids a portion of the pterygoideus passed around below the mandible to insert on the lateral face of the articular. Because of the position and large size of the pterygoideus, its contraction tended to force the jaw rami medially, but the transverse process of the pterygoid bones probably served as a brace or guide to check this movement. In all theriodonts, with the exception of the cynodonts, the adductor mass arose around the margins of the temporal fenestra and inserted on the dorsal and medial surface of the mandible. The lateral face of the mandible shows no marks of muscle insertion in primitive reptiles. When the jaw was elevated it lay too close to the squamosal to allow room for muscle insertion on the lateral surface.

A distinctive feature of skull evolution in advanced therio-

² In an earlier paper (Crompton, 1963), an attempt was made to trace a progressive decrease in the forces to which the jaw joint was subjected within the therapsids leading toward mammals. An important part of the hypothesis of the progressive decrease was the assumed presence of a superficial masseter of the type suggested by Parrington (1955). However, the absence of a superficial masseter inserting on the reflected lamina would not invalidate the general arguments submitted in the paper, because the orientation of the pterygoideus was similar to that of the superficial masseter which was incorrectly assumed to have been present in pre-Triassic therapsids. It is now clear that a true mammalian superficial masseter only came into being in the fairly advanced cynodonts (e.g., *Thrinaxodon*) and that the development of an angle on the dentary in cynodonts is related to the presence of a superficial masseter. Cynodonts are the only theriodonts which developed a major external adductor mass which inserted on the lateral surface of the dentary. This is a basic distinction between the cynodonts and all other theriodonts (dicynodonts excluded); on the basis of present knowledge it precludes all theriodonts, with the exception of the cynodonts, from being ancestral to mammals.

donts (particularly cynodonts) and in dicynodonts is a progressive increase in size of the temporal opening, concomitant with reduction of the transverse flange of the pterygoid. These changes indicate increasing bulk of the adductor externus muscle mass and decreasing bulk of the pterygoideus mass. In cynodonts, a progressively larger portion of the adductor externus mass came to lie lateral to the mandible and to insert into its lateral face. The change of position of the muscle mass was accommodated by outward bowing of the zygoma. In later stages, forces exerted on the lateral face of the jaw ramus tended to balance the forces exerted on the medial face by medial parts of the adductor group and by the pterygoideus, and the transverse flange of the pterygoid became less important as a brace for the ramus. Reduction of the transverse flange may therefore be due to the decline of its function as a brace as well as to reduction of the pterygoideus muscle inserting on it. This process probably led to the total loss of this flange in mammals, presumably because forces acting on either side of the ramus balance each other precisely and permit controlled lateral movement of the rami. Development of a tribosphenic molar pattern was possible only in animals with this type of control.

Evolution of the dicynodont jaw musculature paralleled that of the cynodonts in that a portion of the adductor externus mass gained extensive insertion on the lateral face of the mandible. However, lateral insertion was achieved by excavation of the posteroventral cheek region, which produced the effect of upward bowing of the zygoma (Fig. 1C), in contrast to the lateral bowing characteristic of the cynodonts. Since the zygoma became bowed upward rather than outward, the external adductors tended to exert most of their force in the line of the jaw ramus (Fig. 4E) and thus had little tendency to move the jaw ramus inward or outward. Because the pterygoideus was small in dicynodonts, its medially directed force on the jaw ramus was readily balanced by adductor externus fibers inserting on the lateral face of the mandible, and transverse processes of the pterygoid would not be needed to brace the rami. Reduction of the transverse processes was much more rapid than in cynodonts, being very advanced in the early anomodonts *Otsheria* and *Venjukovia* (Olson, 1962) and complete in definitive dicynodonts.

In a number of advanced dicynodonts, such as *Oudenodon* and *Aulacephalodon*, the zygoma is also bowed extensively outward; these forms may well have been capable of fine control of lateral movements of the mandible. This possibility will be discussed in a later paper.

MUSCLE FORCES

Jaw movement results from the directed force of numerous muscles acting on the mandible. The direction of movement is the product of the collective force of one set of muscles interacting with the dynamic resistance of other muscles and the force of gravity, and with the static resistance of articular and occlusal surfaces. Relationships of the various elements to jaw movement vary complexly through time, but specific elements can be singled out as dominating particular phases in a complete cycle of movement. For purposes of analysis, four muscles are considered in their roles as dominant elements: adductor externus medialis and lateralis, pterygoideus, and depressor mandibulae.

Traction lines conform approximately to the anatomical axes of the muscles they represent, and for purposes of analysis are treated as though they indicate the mean direction of the collective force of the muscle. Forces of the external adductors are directed upward and backward along their respective traction lines. Traction lines for these muscles (A.e.l., A.e.m., P.) are shown in Fig. 2. A generalized force diagram of the external adductors is shown in Fig. 2E. Because horizontal motion of the jaw is generally parallel to JT, and because elevation and depression are normal to JT, the force of the muscle (F.m.) directed upward and backward along AE can be dealt with in terms of a horizontal component (F.h.) coincident with JT, and a vertical component (F.v.) normal to JT. Relative magnitudes of vertical and horizontal components of force are related to the total force of the muscle (F.m.) according to the Pythagorean Theorem: $F.v.^2 + F.h.^2 = F.m.^2$.

When JT is considered as a third-class lever, JT is the length of the work arm and JA is the length of the force arm. When J is

the fulcrum, the upward force at the teeth (Fig. 2E) can be computed according to the law of moments,

$$\frac{JA}{JT} \times F.v.$$

T may also be regarded momentarily as the fulcrum when the teeth meet the resistance of the palate; in this case, an upward force at the jaw joint is computed by the formula

$$\frac{AT}{JT} \times F.v.$$

If points A and T coincide (Fig. 2E: E¹ T.), the vertical component is directed entirely against the resistance of the palate and cannot act through a lever arm; in this case, no upward force is exerted on the joint.

Utilizing the restorations shown in Fig. 4, it is possible to estimate the relative bulk of each muscle, which serves as an index of the force of which each muscle is capable. Relative forces exerted by the muscles at various points at different positions of the jaw can be estimated on the basis of the relationships set forth above and illustrated in Fig. 2E.

Relative bulk of each muscle can be expressed as a multiple of the bulk of the smallest, as follows:

a. Depressor mandibulae (D.m.)	1
b. Pterygoideus (P.)	2
c. Putative superficial masseter (S.m.)	2
d. Adductor externus medialis, whole muscle (A.e.m)	8
e. Adductor externus lateralis (A.e.l.)	6

By use of the Pythagorean Theorem, the law of moments, and the estimated bulk of each muscle, the following relative forces can be determined: 1) vertical force at the joint (J); 2) vertical force at the point of bite (T); and 3) horizontal force along the axis of the jaw ramus (TJ and AJ).

During mastication the dicynodont jaw must have assumed several positions in the course of various cycles of movement.

Characteristic positions assumed by the jaw are illustrated in Figure 5. These are:

- Stage 1, depressed, fully protracted (Fig. 5B)
- Stage 2, elevated, fully protracted (beak bite) (Fig. 5C)
- Stage 3, elevated, beginning of retraction (tooth bite) (Fig. 5C)
- Stage 4, completion of retraction (Fig. 5D)
- Stage 5, depressed, beginning of protraction (Fig. 5A).

In stages 2 and 3 the jaw is in essentially the same position, but in stage 2, forces are considered relative to the beak, and in stage 3, relative to the teeth.

In Table 1, vertical force at the joint, point of bite and horizontal forces acting along the mandibular ramus are calculated for each of the adductor muscles at four of the five positions outlined above. Horizontal forces directed toward the joint are given a positive sign. Forces of the pterygoideus are also shown, computed according to Figure 2D. Their horizontal component is directed towards the beak and is therefore given a negative sign. Jaw action may now be analysed in terms of the relative forces of the muscles.

STAGE 1, JAW DEPRESSED, FULLY PROTRACTED (FIG. 5B & 2C). This position marks the beginning of elevation. Because of the low angle at which the adductor externus fibers approach their insertion, the horizontal component of force is very large (Table 1; -13.04) and the vertical forces at the joint (Fig. 2C: J.) and the anterior point of the jaw (Fig. 2C: B.) are small. The horizontal force is resisted at the joint by the stop mechanism of the posteroventral portion of the condylar surface of the articular (Fig. 2C). Consequently, only the vertical component of force can produce movement, and the jaw is elevated; the small magnitude of the vertical component at the point of bite (Table 1; 0.76) rules out the possibility a powerful bite at this stage. The small vertical force at the joint, which would tend to dislocate the articular, was presumably counteracted by friction resulting from the large horizontal component of the external adductors.

STAGE 2, BEAK BITE (FIG. 5C & 2A). Considerable force must have been required for effective shear at the front of the jaws, and because the relative magnitude of the vertical component was

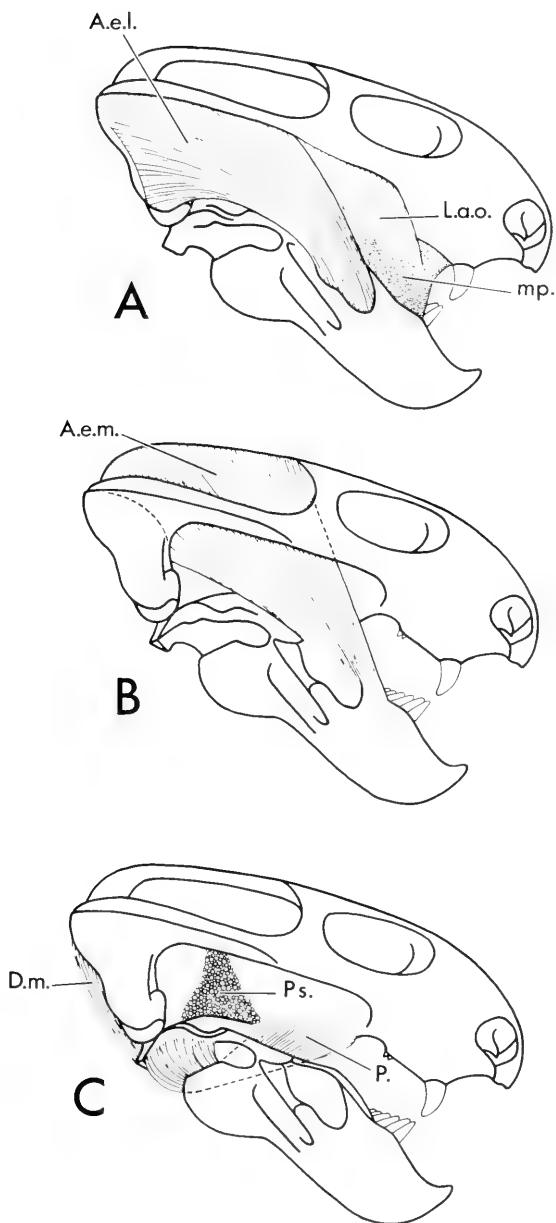
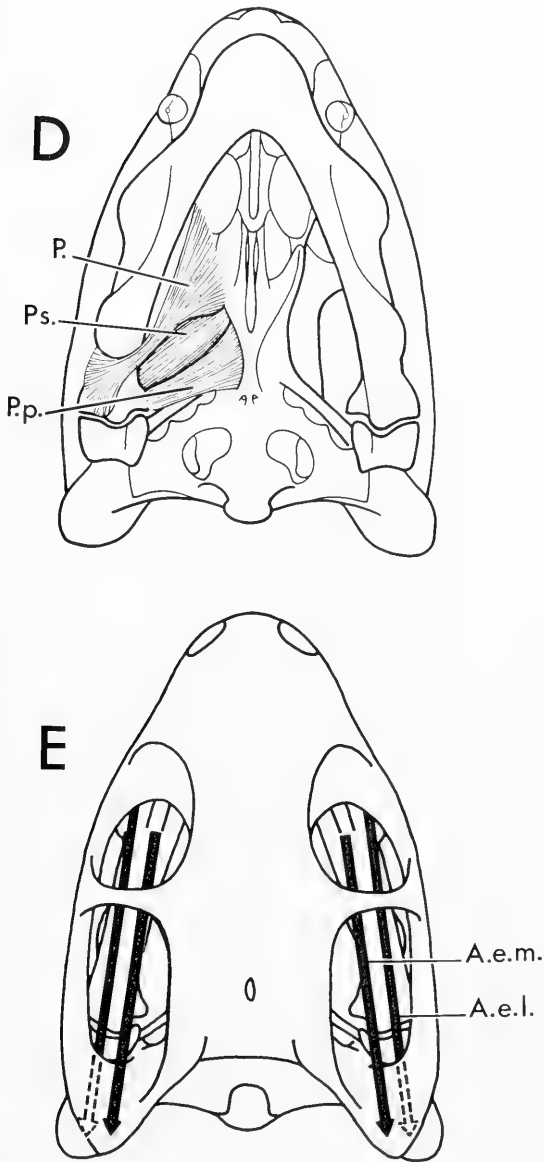


FIG. 4. *Emydops* sp. A-D, reconstructions of the main jaw closing



and jaw opening muscles; E, dorsal view of the traction lines of the two portions of the adductor externus.

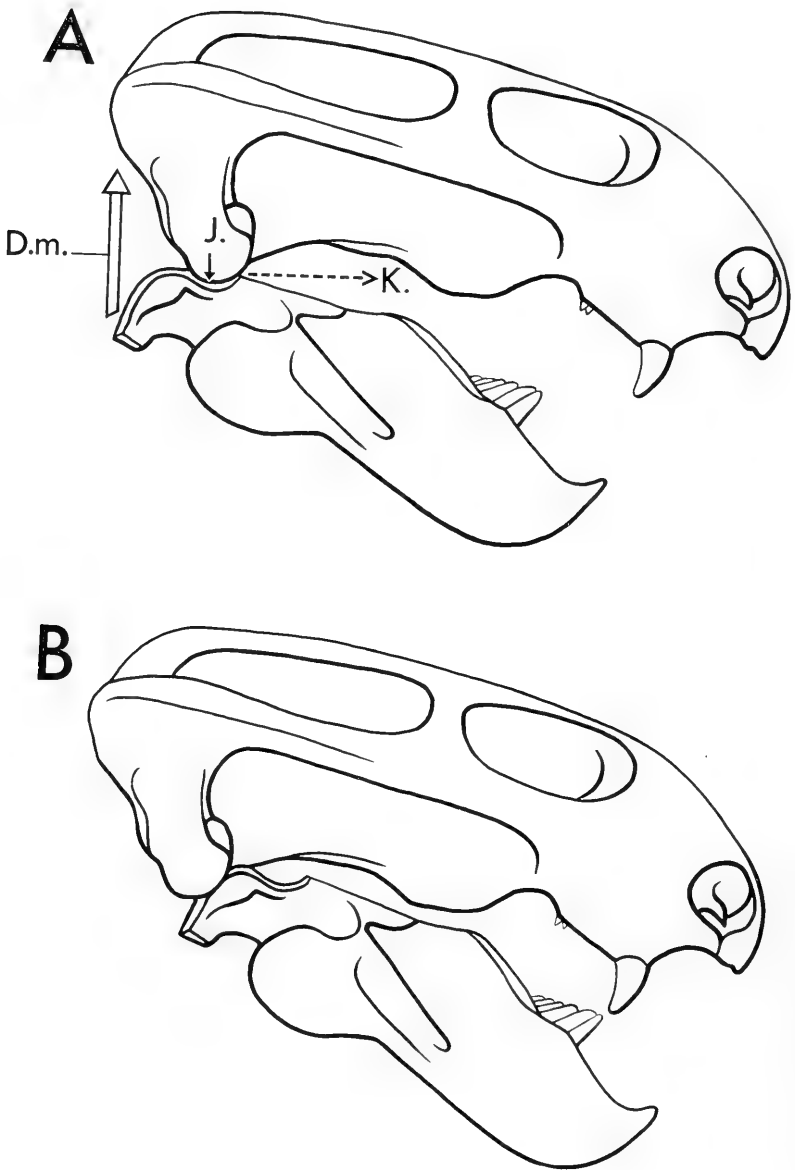
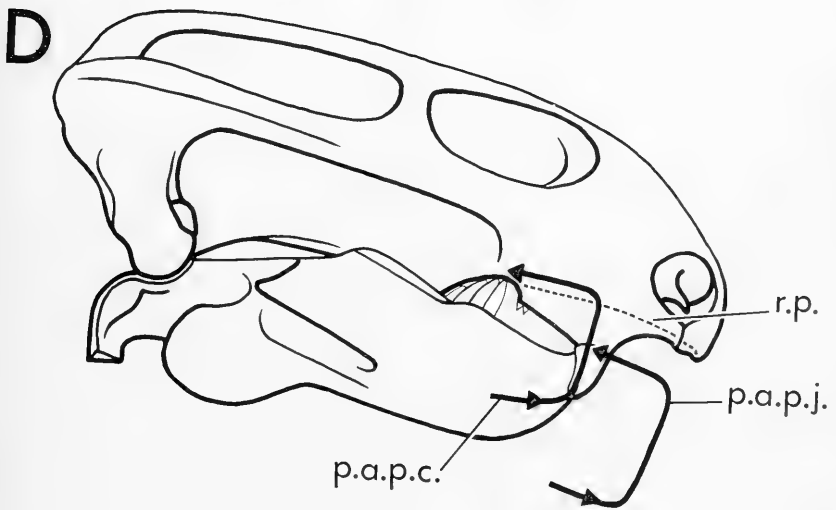
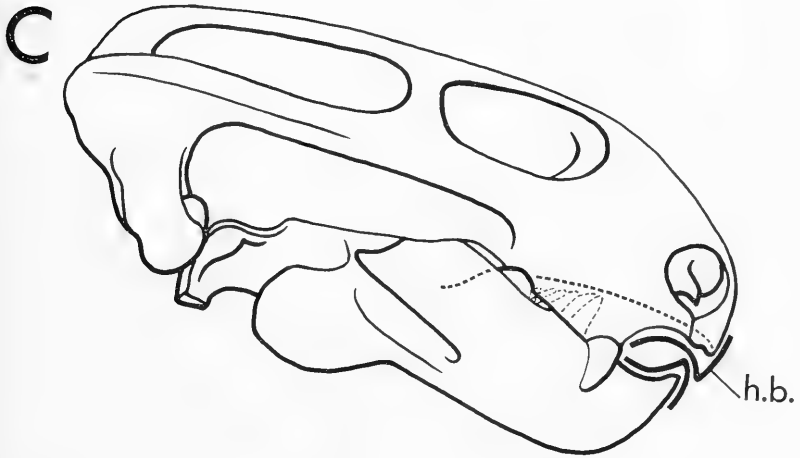


FIG. 5. *Emydops* sp. Lateral views of the skull to illustrate critical stages in the masticatory cycle. A, depression and beginning of protract-



tion; B, full protraction and beginning of elevation; C, beak bite and beginning of retraction; D, complete retraction.

TABLE 1. Muscle forces, weighted by relative bulk and computed according to Figure 2E
(Plus and minus signs indicate jaw elevation and jaw depression, respectively)

LOWER JAW POSITION	DIRECTION OF FORCES	MUSCLE FORCES				
		A.e.m. (8)	A.e.l. (6)	Adductor externus (Total)	Ptery- goideus (2)	"Superficial masseter" (2)
Stage 1, depressed, fully protracted	Vertical (Ant.)	0.04	0.12	0.76		
	(Post.)	0.08	0.06	0.14		
	Horizontal	+7.28	+5.76	+13.04		
Stage 2, beak-bite	Vertical (Ant.)	0.96	0.24	1.20	0.04	0.18
	(Post.)	0.16	0.12	0.28	0.26	0.46
	Horizontal	+6.88	+5.64	+12.52	-1.70	+1.34
Stage 3, elevated, early retraction	Vertical (Ant.)	1.84	0.66	2.50	0.02	0.14
	(Post.)	0.00	0.24	0.24	0.10	0.36
	Horizontal	+6.16	+5.04	+11.20	-1.88	-1.50
Stage 4, elevated, fully retracted	Vertical (Ant.)	3.44	1.38	4.82	0.00	0.00
	(Post.)	0.00	0.54	0.54	0.12	0.26
	Horizontal	+4.56	+4.08	+8.64	-1.88	-1.74

small (Table 1; 1.20) it was necessary to have exerted the full force of the external adductors during beak bite. Traction lines of the lateral external adductor and most of the medial external adductor converged toward the beak at a low angle (Fig. 2A), and the vertical component of force was applied close to the point of bite at the front of the jaw. Therefore, the vertical force working through the beak was about 4.5 times larger than that acting through the joint. Nevertheless, the vertical force at the back of the jaw would have tended to dislocate the joint, except that in Stage 2 the contact between the curved surfaces of the articular and quadrate (Fig. 3A) would permit the larger horizontal force to drive the articular backward and downward below the quadrate, thereby preventing dorsal dislocation. However, immediate retractive movement would have prevented an effective bite at the tips of the beak, and the problem at this stage was not dorsal dislocation of the joint, but premature retraction. As discussed above, the relatively small pterygoideus inserted near the articulation; it exerted more than six times as much vertical force at the joint than at the beak (Table 1) and was therefore not effective in mastication at this stage. On the other hand, because of its large vertical component acting at the joint, contraction of the pterygoideus would have prevented the articular from sliding down the quadrate, and retraction could not have been initiated until the pterygoideus relaxed. Under these circumstances, the full force of the external adductors could be brought into play continuously or intermittently during beak bite for as long as was necessary to accomplish the function of beak bite. This can be adequately demonstrated in a model in which the relative strength and orientation of the muscles are represented by taut elastic bands.

STAGES 3 AND 4, RETRACTION (FIG. 5D & 2B). In this stage, food in the mouth was gripped by the upper teeth and broken up by drawing the lower teeth in a posterior direction through the food. Relaxation of the pterygoideus would have allowed the horizontal component of force of the external adductors to have moved the jaw backward against great resistance. Because the horizontal component of the external adductors was the largest force to which the jaw was subjected, retraction appears to have been the most effective cutting movement during mastication, and

must have enabled the teeth to cut through extremely tough material. The magnitude of the vertical forces would have been sufficient to keep the teeth set firmly in the food being comminuted, but would have been small enough to pose no hindrance to retraction in early stages.

As retraction progressed to its final point (Fig. 5D), vertical force at the teeth increased at the expense of horizontal force (Table 1), driving the teeth ever more firmly into the food material. At the same time, the vertical force at the joint also increased, but the joint had moved toward a condition of vertical stability (quadrate condyle resting in the condylar recess) so that there was no risk of dislocation with increased vertical force. However, the increased total vertical force may have played a part, in association with the shape of the condylar recess and of the back of the palate, in terminating retraction.

STAGE 5, DEPRESSION AND PROTRACTION (FIG. 5A & 2D). At the end of retraction, relaxation of the adductor externus group and contraction of the pterygoideus would have resulted in the jaw being drawn forward with the teeth held against the palate. The values of force of the pterygoideus (and a putative superficial masseter—S.m.) shown in Table 1 are computed on the same basis as the force of the external adductors (Fig. 2D), but with the traction lines directed upward and forward rather than upward and backward. The sequence of stages for the pterygoideus acting in protraction should be read in reverse order from Stage 4 to Stage 2 in Table 1.

It has already been pointed out that such movements would not have been very effective in cutting food because the anterior surfaces of the teeth are blunt. In addition, the vertical force acting through the teeth as a result of contraction of the pterygoideus was at most about $1/5$ of the vertical force at the joint, and from about $1/30$ to $1/100$ the vertical force acting through the teeth as a result of the contraction of the external adductors. If the bite force resulting from contraction of the pterygoideus were to have approached that caused by the external adductors at the beginning of retraction, its vertical force at the joint must have been of fantastic magnitude, and would have increased as the joint became less stable (Table 1: Stages 3 and 2). Such a force would have had an increasing tendency to dislocate the joint as the jaw moved

into protraction; the only way dislocation could have been prevented was by simultaneous contraction of the external adductors, which would then have also stopped protraction.

Thus, functional analysis confirms the evidence of anatomy that the pterygoideus must have been small, and that no effective cutting stroke was delivered during protraction. The presence of a superficial masseter such as that proposed by Cox (1959) and Ewer (1961) would do nothing to change this conclusion. Morphologically, a superficial masseter could not have been much more bulky than the pterygoideus, and this traction line would have been similar. Two such muscles could not have delivered a force at the teeth comparable to that of the external adductors, and the objections to the presence of a strong pterygoideus are equally applicable to a strong superficial masseter. At most, a weak superficial masseter may have helped the pterygoideus stabilize the joint against premature retraction during beak bite, and might have aided in normal protraction (see below). However, protraction probably took place against no resistance except the inertia of the jaw, and therefore did not require great force. The pterygoideus was probably quite capable of accomplishing the task by itself.

Normal protraction probably took place only after depression was initiated, and the pterygoideus and depressor mandibulae functioned as agonists during the process. Line JB does not pass through the insertions of these muscles (Fig. 2D), and so they must be regarded as acting through bell-crank arms (Fig. 2F & 2D: I.P.-J., I.D.m.-J.). From this viewpoint they are antagonists — the pterygoideus producing elevation and the depressor mandibulae producing depression. The bell-crank arms are radii of the same circle, with a center at the contact point between articular and quadrate (J.). The traction line of the pterygoideus (P.) is very nearly tangential to this circle, so essentially all of the force of the muscle is exerted in elevation. However, this force must move the symphysis of the jaw upward against gravity. Upward force at the beak is delivered through a first-class lever, and its value is therefore expressed by the law of moments,

$$\frac{I.P.-J.}{JB} \times F.m.$$

The depressor mandibulae, on the other hand, acts with gravity

rather than against it, and the lever effect of the jaw becomes irrelevant. However, the traction line of the depressor is not quite tangential to the circle of rotation around the joint, and only the tangential component (F.t.) is effective in depressing the jaw. Components of force of the depressor mandibulae are computed by reference to the Pythagorean Theorem: $F.t.^2 + F.r.^2 = F.m.^2$. Force values of the pterygoideus and depressor mandibulae computed on the basis of Fig. 2F are recorded in Table 2; the negative sign for the depressor signifies depression of the jaw.

Values of the forces of the pterygoideus and depressor mandibulae computed by the foregoing procedure are applicable only when the jaw is being depressed. However, those of the pterygoideus probably correspond more closely to reality than the values listed in Table 1, which are intended only to show what the forces of pterygoideus would be if the muscle functioned in a manner comparable to the external adductors.

At the end of retraction (Fig. 5D), the external adductors relaxed, and the depressor mandibulae and pterygoideus contracted simultaneously. Aided by gravity, the depressor mandibulae was able to overpower the pterygoideus (Table 2, vertical force), and the jaw was depressed (Stage 5, Fig. 5A). Once the jaw was depressed, the line along which the articular could move most readily (Fig. 2D & 5A: JK) no longer coincided with the longitudinal axis of the ramus, but was nearly parallel with the traction line of the pterygoideus. Virtually all of the force of the pterygoideus was therefore applied to protraction (Table 2, horizontal force). Although the depressor could overpower the elevating effect of the pterygoideus, it could not prevent forward motion; the pterygoideus therefore probably drew the jaw forward during protraction while the depressor held it in a depressed position. This motion continued until the jaw reached the position described as Stage 1 (Figs. 2C & 5B). It was terminated by increasing contraction of the external adductors, which ultimately overpowered the pterygoideus to initiate a new cycle.

Movements of the lower jaw may be summarized as follows: 1) depression, 2) protraction, 3) closing in a protracted position, which results in beak bite, 4) retraction, during which the composite blade formed by the lower teeth was drawn forcibly backward through food held in the mouth. In life, beak bite and the

TABLE 2. Muscle forces, weighted by relative bulk and computed according to Figure 2F

(Plus and minus signs indicate jaw elevation and jaw depression, respectively)

LOWER JAW POSITION	DIRECTION OF FORCE	MUSCLE FORCES		
		Pterygoideus (2)	Depressor mandibulae (1)	"Superficial masseter" (2)
Stage 4, elevated, fully protracted	Vertical	0.47	-0.65	0.36
	Horizontal	-2.00		?
Stage 5, depressed, slightly protracted	Vertical	0.30	-0.78	0.32
	Horizontal	-2.00		?

cutting action of the teeth by a retractive movement were probably distinct. Tough food held in the mouth was probably sliced to small pieces by a series of rapid retractive movements consisting of slight depression, full protraction, and followed by elevation and powerful retraction. This movement would resemble that which characterizes chewing in rodents except that in these forms the power stroke is an anterior one.

MASTICATORY APPARATUS IN *LYSTROSAURUS*

In *Lystrosaurus* the masticatory apparatus is basically similar to that of a large variety of dicynodonts, for example: *Kan-nemeyeria*, *Daptocephalus*, *Placerias*, some species currently assigned to *Dicynodon*, and the middle Triassic dicynodonts of East Africa. *Lystrosaurus* was selected for a study of jaw movements of advanced dicynodonts because undistorted specimens that can be prepared in acid are available. The following description is based on a skull in the South African Museum (S.A.M. 4325).

ANATOMY OF THE JAWS

With the exception of the upper caniniform tusks, no teeth are present in *Lystrosaurus* (Fig. 6C & F, 7D). The sharp marginal rim of the maxilla and premaxilla is more prominent than in *Emydops*, especially just anterior to the tusks where the anterior margin curves downward well below the level of the premaxillary rim. The medial surface of the tusk is flush with the medial surface of this outer rim (Fig. 6D & 7H). Anteriorly, the medial surface of the rim of the palate supports two palatal ridges (Fig. 6F) which project a short distance below the ventral margin as seen in lateral view (Fig. 6A). These ridges are present but less prominent in *Emydops*. For comparison, the lower jaws of *Emydops* and *Lystrosaurus* in Figure 7 have been drawn so that the distance between the posterior surface of the articular and the anterior termination of the longitudinal groove of the dentary is the same in both cases. The symphyseal region is longer and more massive in *Lystrosaurus* than in *Emydops* (Fig. 7E & F). Anterior to the teeth, the dorsal border of the lower jaw of *Emydops* drops away gradually to form a fairly delicate beak (Fig. 7E). In

Lystrosaurus, on the other hand, the symphyseal region has been reinforced and strengthened so that in lateral aspect it is extremely deep and the dorsal border of the mandible in *Lystrosaurus* is built up to a line nearly coinciding with the apices of the lower teeth in *Emydops* (Fig. 7E). The symphyseal region of *Lystrosaurus* (Fig. 7D) has a rectangular appearance in dorsal aspect because the outer faces of the dentaries anterior to the insertions of the external adductor muscles are nearly parallel to each other. In *Emydops* the lateral surfaces of the dentaries converge anteriorly (Fig. 7B). In *Lystrosaurus* the sub-parallel lateral dentary faces fit closely against the vertical rim of the palate (Fig. 6D & E).

The dorsal surface of the dentary, between the anterior termination of the longitudinal groove and the upturned tip of the beak, consists of two broad, flat surfaces (Fig. 7D: d.t.) separated by a deep medial groove (m.gr.). These surfaces are termed the dentary tables and are not present in *Emydops*. The anterior terminations of the dentary tables are produced upwards to form short, sharp processes (lat. ant. proc.) similar to the well-developed processes present in this region in *Emydops*. The tip of the beak is also produced upward in the midline, forming a median process (m. proc.).

As in other dicynodonts, the bone surface of the external face of the symphyseal region, the dentary tables, and much of the periphery of the palate, including its outer rim, is perforated with nutrient foramina, and for this reason is presumed to have been covered with horn. The configuration of the horny covering must have conformed to that of the underlying bone; the covering of the dentary tables was broad and flat, while that of the palatal rim formed a sharp, blade-like edge. The horn covering the tip of the beak terminated in a sharp leading edge which probably bore a median as well as two lateral processes.

The ventral surfaces of the palatines and adjoining region of the maxillae in *Lystrosaurus* are penetrated by many large and small foramina. Because of the great number of foramina and the enormous variety in size, the ventral surfaces of the palatines and maxillae are uneven and form a series of irregular bumps, which in mechanically-prepared specimens appear as a system of tubercles. Only by acid preparation is the perforate nature of these areas revealed. The numerous foramina penetrating the palatines are a

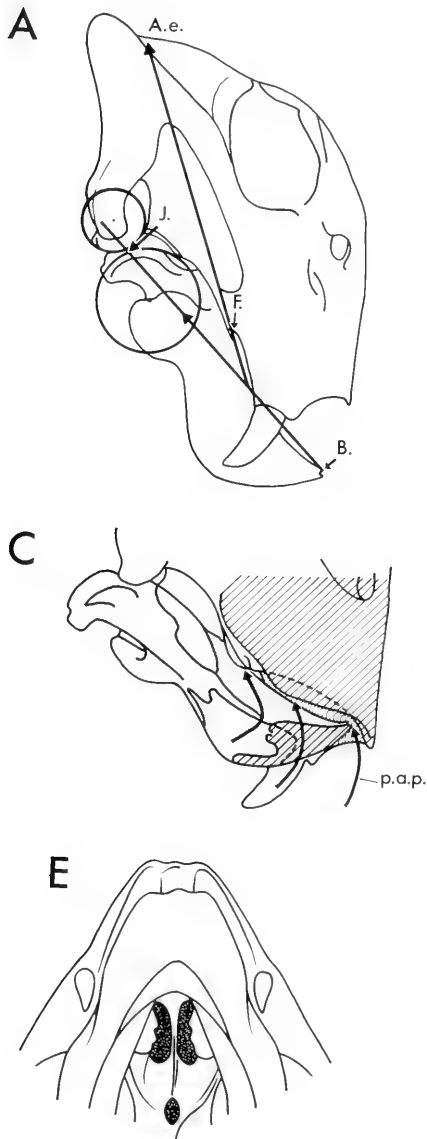
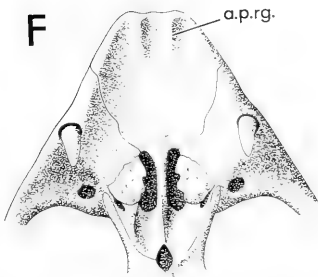
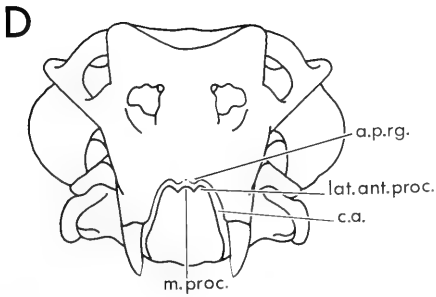
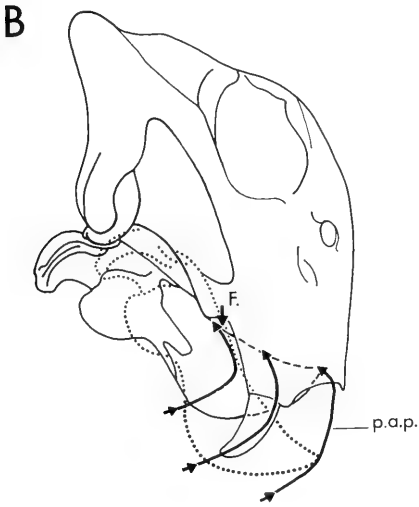


FIG. 6. *Lystrosaurus* sp. A, lateral view of the skull to illustrate the traction line of the adductor externus (A.e.), the radii of the arcs of the articular surface forming the jaw joint and the functional axis of the lower jaw (JB). B, movement of the lower jaw from complete protraction to complete retraction. C, sagittal section of the snout to illustrate



the relationship of the symphysis of the lower jaw and outer rim to the palate. D, anteroventral view of the skull to illustrate the cutting area (c.a.) between the symphysis and outer rim of palate and canine. E, ventral view of palate with lower jaw in position and F with lower jaw omitted.

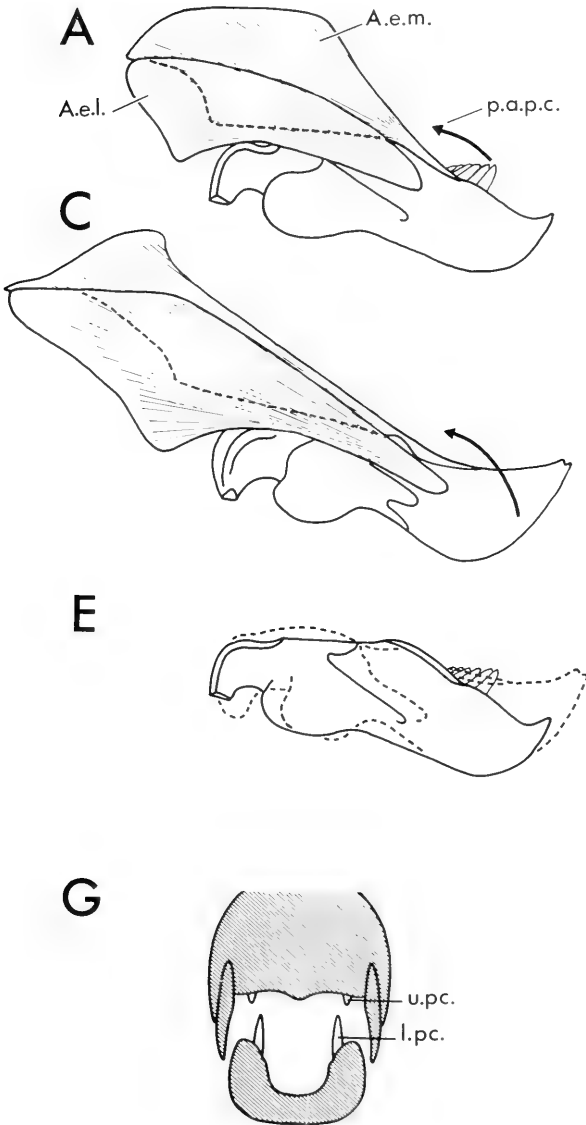
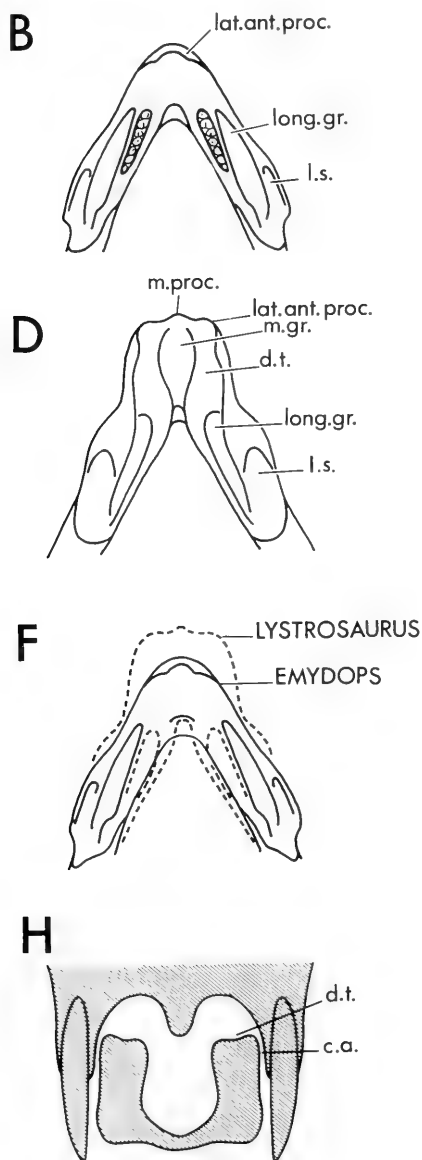


FIG. 7. Comparison of the lower jaws of *Emydops* and *Lystrosaurus*. A, lateral view of lower jaw of *Emydops* and reconstruction of adductor externus; B, dorsal view of anterior half of *Emydops* lower jaw; C, lateral view of the lower jaw of *Lystrosaurus* and reconstruction of the two adduc-



tors; D, dorsal view of anterior half of *Lystrosaurus* lower jaw; E, comparison of the lateral views of the lower jaws; F, comparison of the dorsal views of the lower jaws; G and H, section through the snouts of *Emydops* and *Lystrosaurus*, respectively.

clear indication that the ventral surface was covered by a substantial layer of horn. Ewer (1961), in a study of the late Permian dicynodont *Daptocephalus*, suggested that the outer walls of the longitudinal groove on the dorsal surface of the dentary were opposed to the richly vascularized area of the palatine and maxilla to form a cutting and crushing mechanism. However, the walls of the longitudinal groove did not bite against the vascularized area of the palate in *Lystrosaurus*, and because of the strong structural resemblance of *Daptocephalus* to *Lystrosaurus*, we cannot accept Ewer's thesis.

The jaw joint of *Lystrosaurus*, like that of *Emydops*, is typically dicynodont and permits a long range of fore-and-aft travel. However, the posterior ventral articular facet, characteristic of the jaw joint of *Emydops* and some other small dicynodonts, is absent in *Lystrosaurus*. Instead, the convex middle portion of the articular surface continues onto the posterior surface. The radius of the arc of this portion of the articular surface is much larger than the radius of the arc forming the articular surface of the quadrate condyle (see Fig. 7A).

The external adductor musculature is similar in most respects to that of *Emydops* (Fig. 7A & C). In both, the adductors approach the dentaries at similar angles.

JAW FUNCTION

In *Lystrosaurus*, as in *Emydops*, the convex surfaces of the joint form an inclined plane, so that the articular slid down the anterior face of the quadrate when the jaw was retracted by the force of the external adductors. In both genera, the horizontal component of force of the external adductor muscles was by far the largest single component of the trigeminal muscular system, and provided the posteriorly directed power stroke of mastication.

During elevation of the jaw of *Lystrosaurus*, the dorsal edge of the mandible at the longitudinal groove was brought into contact with the ventral border of the maxilla just behind the tusk (Fig. 6A: F) before jaw closure was complete. The only way the jaw could be closed further, once it had reached the position shown in Figure 6A, was by retraction, during which its dorsal margin was held firmly against the maxilla at point F. by the vertical

component of the external adductors. As retraction progressed, the back of the jaw was forced downward quite a long distance because of the size of the radius of the curved articular surface (Fig. 6B). The mandible rode against point F., which acted as a fulcrum, and, as a result, the tip of the beak moved upward in proportion to the downward movement of the back of the jaw.

Numerous articulated and undistorted specimens of *Lystrosaurus* indicate that close contact was possible between upper and lower horny beaks. In Figure 6B three arbitrarily selected points on the dorsal surface of the dentary illustrate the movement of the lower jaw during elevation and retraction. As the jaw approached the retracted position, the square anterior edge of the lower beak passed close to the anterior wall of the palate, its processes (Fig. 7D: m. proc., lat. ant. proc.) intermeshing with the ridges and grooves of the palate (Fig. 6E). Relationships between the tip of the lower beak and the anterior wall of the palate during this action are shown in sectional view in Figure 6C. The flat outer surfaces of the symphyseal region (Fig. 6D: c.a.) passed upward and backward in close application to the vertical inner surfaces of the deep palatal rims, the anteroventral edges of which were sharp. This must have formed an extremely effective cutting mechanism, similar in principle to a guillotine. Simple depression and elevation of the lower jaws in a retracted position, i.e., without utilizing retractive movement, would have produced a cutting action between the ventral edges of the palatal rim and the symphysis, but would not have permitted contact anteriorly, between the tips of the jaws. Cutting action at the tips of the jaws required that the lower jaw be elevated and retracted simultaneously, which was accomplished by the "rocking" action of the mandible about point F.

The flat surfaces of the dentary table cannot be opposed to the arched surfaces of the palate (Fig. 7H). There was, therefore, no possibility of a grinding action between the lower jaw and palate as described by Camp and Welles (1956) in *Placerias*, or by Ewer (1961) in *Daptocephalus*. The masticatory apparatus of *Lystrosaurus* was essentially one adapted to cutting and not to grinding.

Detailed analysis of muscle forces in *Lystrosaurus* is unnecessary because they are basically similar to those of *Emydops*. When

the jaw was protracted, the traction lines of the external adductors (Fig. 6A: A.e.) acted through the pivot point (F.) of the lower jaw. As a result, the vertical component was exerted against resistance provided by the maxilla and could have no effect on either the joint or the beak. The entire force of the horizontal component was effective at the beak, producing the motion described above, in which elevation and retraction were combined by means of the rocking of the mandible about point F.

This combination permitted the tremendous force of the external adductors to be utilized much earlier in the masticatory cycle, and contrasts with the beak bite system of *Emydops*. In beak bite, the horizontal component was employed, in conjunction with the posteroventral facet of the articular, to stabilize the jaw in early phases of the cycle; the only effective shearing force at this time was delivered by the relatively weak vertical component. Utilization of the horizontal component in shearing was restricted to the posterior area occupied by the dentary teeth and took place at a distinctly later phase of the cycle. In *Lystrosaurus* there was no distinct beak bite because no posteroventral facet was developed on the articular. The posterior shearing area of the teeth was replaced functionally by the deepening of the palatine rims in front of the tusks (Figs. 7G & H). This area lies further forward than the teeth of *Emydops* and is continuous with the beak. It was brought into play by the same combination of retracting and elevating motion that brought the tips of the beak together, the entire action being powered by the horizontal component of force of the external adductors.

DISCUSSION

The conclusion of Watson and others that the dominant movement of the jaw in dicynodonts was anteroposterior is amply confirmed by the two genera studied in detail in this paper, and by many other forms examined more cursorily. However, the shape of the postcanine teeth (when present) and the structure of the joint in relation to size and attachment of muscles indicate that the jaw was effective in breaking up food only when being retracted in an elevated position. Protraction was closely associated with depression and served primarily to return the jaw to a forward

position in preparation for the next retractive stroke. Morphology of the portions of the upper and lower jaws that were opposed to each other confirm this interpretation, and indicate further that the chief means of comminuting food was by shearing. No evidence of a grinding or crushing function was found in the present study.

The two forms considered illustrate contrasting modifications of the basic dicynodont mechanism. In *Emydops*, the cutting area at the front of the beak is distinct from the more posterior cutting area between dentary teeth and palate. The anterior cutting area is brought into play at the beginning of the cycle by a primarily vertical component of motion and force. The posterior cutting area comes into play slightly later, at which time motion and force are primarily horizontal (retractive). In *Lystrosaurus*, on the other hand, the distinct posterior cutting area has disappeared, and is replaced functionally by blade-like expansions of the maxillae which are continuous with the beak. *Lystrosaurus* thus has a single broad cutting area at the front of the jaws, which is utilized as a unit throughout most of the cycle; elevation and retraction of the mandible are combined in a single motion which is actuated primarily by the very powerful horizontal component of the external adductor group of muscles.

Because of our inadequate understanding of the great diversity of dicynodonts as a whole, the phylogenetic significance of these differences must be approached with caution. However, a few tentative conclusions may be drawn. The specimen of *Emydops* studied is from the upper part of the Lower Beaufort, but pristerodonts very similar to it are known from the oldest fossil-bearing beds of the Beaufort. If pristerodonts are truly primitive, as they seem to be, the retention of a distinct beak bite, actuated by a vertical component of force, may be interpreted as an inheritance from a pre-dicynodont condition in which the typical retractive power stroke had not yet been developed. The presence of functional postcanine teeth is likewise an archaic character, retained from an animal in which the primary bite force was provided by a vertical component. The pristerodonts are the earliest known forms in which the retractive force of the external adductors was used effectively.

Lystrosaurus is from the Middle Beaufort, but its type of jaw mechanism is already evident in forms such as *Dicynodon feliceps*,

a contemporary of *Emydops* from the upper part of the Lower Beaufort. There are no forms with a *Lystrosaurus* type of jaw mechanism known from the oldest fossiliferous beds of the Beaufort, and the animals of that age that most nearly resemble *D. feliceps* and *Lystrosaurus* have many features of the jaw mechanism similar to those of pristerodonts. From the evidence of both morphology and temporal occurrence, therefore, it is possible that the line leading to *D. feliceps* and *Lystrosaurus* may have been derived from an early pristerodont, very early in or just prior to Beaufort time. Evolution to the *Lystrosaurus* level of organization consists primarily of transferral of all cutting action to the front of the jaws, and combination of elevation and retraction into a single motion; it probably evolved primarily by the selective value of complete utilization of the powerful horizontal component of force.

There is no question but that *Lystrosaurus* could exert a much more powerful cutting force at the front of the beak than could *Emydops*. This should be interpreted as much in terms of the different kinds of food eaten by these animals as in terms of a general tendency toward increasing efficiency. During most of the interval in which the *Lystrosaurus* line was perfecting its jaw apparatus, pristerodonts such as *Emydops* were surviving successfully with their archaic mechanism. Whatever the ecological niche for which *Emydops* was adapted, it must have remained available throughout the Lower Beaufort.

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KEY TO ABBREVIATIONS

- A.e. — traction line, adductor externus (not differentiated)
 AE, TE — traction lines of adductor externus in force diagrams
 A.e.l. — adductor externus lateralis
 A.e.m. — adductor externus medialis
 a.p.rg. — anterior palatal ridge
 B. — contact between tips of horny beak
 c.a. — cutting area
 cen.c.art. — central convex portion of the articulating surface of the articular
 con.rec. — condylar recess
 C.S. — radius of the convex portion of the articulating surface of the articular
 D.m. — depressor mandibulae
 d.t. — dentary table
 ep. — ectopterygoid
 F. — fulcrum upon which mandible rocks during closure
 F.h. — horizontal component of force
 F.m. — total force of muscle
 F.r. — radial component of force
 F.t. — tangential component of force
 F.v. — vertical component of force
 h.b. — horny beak
 I.D.m. — insertion, depressor mandibulae
 I.P. — insertion, pterygoideus
 J. — contact between surfaces of articulation at joint
 JT (or JB) — longitudinal axis of jaw ramus
 K. — direction of movement of the lower jaw

- lat.ant.proc. — lateral anterior process of the mandible
 L.a.o. — levator angularis oris
 l.c. — lateral condyle of the articular
 L.C.S. — length of condylar surface
 long.gr. — longitudinal groove
 l.pc. — lower postcanine teeth
 l.s. — lateral shelf of dentary
 m.c. — medial condyle of the articular
 m.gr. — medial groove
 mp. — *Mundplatt*
 m.proc. — medial anterior process of the lower jaw
 p. — palatine
 P. — pterygoideus
 pal.r. — anterior rim of the palate
 p.a.p. — paths of three arbitrary points on dorsal surface of mandible during closing of jaws
 p.a.p.c. — path of anterior lower postcanine during jaw closing
 p.a.p.j. — path of anterior point of jaw during jaw closing
 P.p. — adductor internus, "pterygoideus posterior" slip
 Ps. — adductor internus, pseudotemporalis
 pt. — pterygoid
 p-v.art. — posteroventral articulating surface of the articular
 q. — quadrate
 q.j. — quadratojugal
 Q.S. — radius of the convex portion of the articular surface of the quadrate
 r.l. — reflected lamina of angular
 r.m. — reflected margin of squamosal
 r.p. — roof of palate
 r.proc. — retroarticular process
 S.m. — putative superficial masseter
 sq. — squamosal
 T. — contact between dentary teeth and palate
 Td and Td¹ — total horizontal distance traveled by the lower jaw during mastication
 u.pc. — upper postcanine teeth

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