Morphological Basis of the Feeding Mechanics in the Shingle-Back Lizard *Trachydosaurus rugosus* (Scincidae, Reptilia)

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ABSTRACT   This report details certain morphological aspects of the feeding system of the lizard *Trachydosaurus rugosus*, an opportunistic omnivore, as a first step toward a functional characterization of its masticatory system. The skull is relatively solid and internally well braced; its anterodorsal elements are tightly tied to the integument and covering osteoderms. There is potential for intracranial kinesis and streptostyly. At small gapes, mandibular movements seem to be restricted to relatively simple, hingelike actions by a series of mechanical stops. The dentition features a progression of smaller to larger teeth posteriorly along the tooth row. The jaw adductor musculature is massive; other jaw muscles are relatively simple. The external adductor mass is particularly noteworthy in that it is subdivided into four mechanical units by a complex internal tendon tract (the coronoid aponeurosis). The internal adductor is composed of two separate gross muscles, pseudotemporalis (PST) and pterygoideus (PT). Each of these is subdivided into two main units by aponeurotic sheets, the PST by parts of the coronoid aponeurosis and the PT by a separate series. The form of the aponeurotic system in *Trachydosaurus* confounds the separation and identification of the adductor muscles and their component parts along the lines of traditional nomenclature, and underscores the need for separating criteria based on homology from those reflecting morphological and possibly functional divisions.

The shingle-back skink, *Trachydosaurus rugosus*, is a locally common lizard in Australia. Although various of its populations range across the continent between 23° N. and the southern coast and onto coastal islands (Cogger, '75), the distinctness of the genus has recently been questioned and the species reassigned to *Tiliqua* (Hutchinson, '81). The extensive range and the rather diverse habitats occupied by this lizard are paralleled in its omnivorous food habits. Stomach contents of wild specimens indicate that the shingle-back takes "insects and other arthropods, snails, carrion, flowers, fruit and berries" (Cogger, '75). Farmers complain about its interest in tomatoes, and in West Australia it feeds on the introduced snail *Helix pulmonata*.

The size, ease of handling, and availability of *Trachydosaurus* have made it the animal of choice for multiple physiological studies. Consequently, it appeared of interest to analyze its feeding system, both to characterize how an omnivore deals with a variety of food types and to permit comparison with the motor sequences in the mandibular musculature of *Sphenodon* (Gorniak et al., '82). The present report deals with the skeleton, aponeuroses, and cephalic musculature involved in feeding. It concentrates on those muscles that may be involved in moving the jaws, omitting the hyoid, lingual, ocular, and cervical musculature, and detailed joint morphology. It aims to provide a basis for a functional characterization of the masticatory system.

MATERIALS AND METHODS

The morphology of *Trachydosaurus rugosus* was analyzed from 1) three prepared skulls loaned by the Department of Zoology, University of Western Australia and 2) dissection of eight specimens, two provided by the Museum of Western Australia and the others part of a series previously used for

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experiments. All had been collected in the vicinity of Perth. One prepared skull and one dissection specimen were treated with oil of cloves in order to clear the bones and confirm fusion of cranial elements. Dissection proceeded in two directions: 1) starting from the outside after removal of the skin and osteoderms, making sure to note the tendinous insertions to the underside of the skin, and 2) from the inside, utilizing animals which had been frozen and sawed either sagitally or transversely. Descriptions note angles estimated with the mouth closed and the head extended straight anteriorly. During display or some bites, the skull may be elevated more than 45° from the horizontal; for functional analyses, the action lines of muscles should be checked by comparing them among specimens with the mouth closed and those preserved with the mouth open. The individual muscles were dissected by layers, both mechanically and chemically by the application of Clorox (sodium hypochlorite) to dissolve connective tissues. The preparations were then stained with methylene blue or iodine (Bock and Shear, '72) to identify muscle fibers and characterize fiber direction. The potential for intracranial kinesis was determined through manual manipulations of the skull and dissected specimens. Approximate fiber lengths were obtained by measuring fiber bundles with a millimeter ruler during dissection.

Connective tissues
The skeleton (Fig. 1)

The skull of *Trachydosaurus rugosus* has been well illustrated, but only briefly described (Brühl, 1886, pl. CXLIX, Figs. 10, 13–19, note that numbers and species assignment in figure captions confuse some views with those of *Sphenodon*). Sometimes the skull is mentioned in comparison with that of the closely related species *Tiliqua scincoides* in taxonomic discussions of the Scincidae (e.g., Camp, '23; Greer, '70). The cranial elements are for the most part tightly sutured or fused, thus producing a relatively solid, internally well-braced cranial frame. The present discussion will focus on those structures thought to be significant for the functional analysis or denoted as important taxonomic features by Greer ('70). General terminology of bones follows Oelrich ('56) and Romer ('56).

The facial bones (premaxillae, maxillae, nasals, frontal, prefrontals) are well inter-

digitated and may be locally fused with each other in adults; they are secondarily reinforced by a heavy external layer of thick osteoderms. Part of the internasal suture is fused. The single frontal shows a median fusion line (fl, Fig. 1A) marking the junction of originally paired elements; it is also partially fused with the parietal. The prefrontal is fused to the postorbitofrontal, thus forming a solid arch of bone along the dorsal margin of the orbit.

There is some confusion concerning the nature of the postfrontal and postorbital in the Scincidae. These bones may be separate elements, may be fused, or one (usually the postorbital) may be absent (Camp, '23; Greer, '70; Romer, '56). Whereas the relationship of the bones to each other and to the squamosal is taxonomically important (Greer, '70) it is often uncertain which element persists or whether fusion has taken place (Romer, '56). In *Trachydosaurus*, the region back of the orbit is occupied by a single, large bone. For present purposes, it is simplest to adopt the terminology of Rieppel ('81) and name the bone, which extends from the dorsoposterior margin of the orbit to the small, slitlike supratemporal fossa, a postorbitofrontal. This bone articulates with both the parietal and the squamosal, thus forming a complete supratemporal arch (*sensu* Greer, '70).

The unpaired parietal occupies a rectangular area on the cranial roof. A parietal foramen lies in the anterior midline of the parietal plate and penetrates the covering osteoderm. The parietal sends out two processes on each side. The ventral process reaches almost directly ventral from the deep surface near the anterior edge of the parietal plate; the process passes along the anterior edge of the bony braincase and provides reinforcement for its membranous walls. The supratemporal process leaves posterolaterally and curves ventrally to brace the posteromedial edge of the curved, bladelike squamosal. This supratemporal process forms the roof of the posttemporal fossa. More distally, the joined parietal and squamosal bones of the supratemporal process are tightly braced between the paraoccipital process and the mediodorsal portion of the quadrate.

The solidly sutured and relatively immobile palatal shelf is comprised of premaxillae, maxillae, palatines, ectopterygoids, and pterygoids; the anterior palatal vacuity is roofed by shallow vomers that anteriorly base themselves against the palatal processes of

the premaxillae. The palatines join along the midline but the palatal rami of the pterygoids do not. Thus, there is a relatively short secondary palate. The palatine contacts the ectopterygoid at the posteromedial edge of the infraorbital vacuity. Each pterygoid sends out a long, posterolaterally curving quadrate process of J-shaped cross-section with the shallow trough opening mediodorsally. The process terminates in a close tie to the quadrate that allows slight flexibility or sliding. The quadrate process is anteromedially braced against the large, winglike basipterygoid process in a synovial joint that permits some relative displacement. A slender, laterally bowed epipterygoid extends dorsally from a cup-shaped depression in the anterodorsal portion of the quadrate process. The epipterygoid is slightly mobile at both its ventral extent (pterygoid joint) and its dorsal extent (prootic joint).

The anterior braincase is membranous. The bones of the posterior braincase (prootic, opisthotic, basisphenoid, occipital elements) are well fused, thus producing a solid internal element of the skull. The prootic is the main lateral component of the braincase; it sends out an anteroventral, scimitarlike inferior process. The dorsal border of the inferior process forms the ventral margin of the trigeminal notch; the ventralmost convexity is fused to the basisphenoid. More anteriorly, the prootic is solidly connected to the ventral process of the parietal and relatively loosely attached to the dorsal end of the epipterygoid. The supraoccipital sends out a bony anterodorsal process that becomes the cartilaginous cone of the processus ascendens tecti synotici. This process fits into a posteroventrally-facing cup on the posterior edge of the parietal. Some flexibility is possible between the supraoccipital area and the cranial roof at this synchondrosis. The posterolateral aspect of the bony braincase emits the stout paraoccipital wing (mainly an opisthotic element) that connects to the distal end of the supratemporal process and to the dorsomedial portion of the quadrate. Finally, the floor of the braincase is continuous with the above-mentioned basipterygoid process (a basisphenoid element).

The quadrate is large; in lateral view its outline is shaped like an inverted hook. Its anterior face is broad and the dorsal aspect is curved. Dorsomedially, the quadrate is tightly braced by the supratemporal process and the paraoccipital one. Ventromedially,

the quadrate is closely bound to the pterygoid at the quadrate process. The spool-shaped quadratomandibular condyles lie almost horizontal, at the ventral aspect of the quadrate; their enlarged medial portion extends slightly more ventrally.

The bones of the lower jaw are robust and tightly articulated; the junction at the mandibular symphysis is capable of only limited flexibility. The coronoid process projects dorsomedially and sends a heavy ridge from its apex down the medial aspect of the coronoid bone. The apex of the process houses a cuplike fossa and the lateral part of the process is shelflike. The lateral and medial aspects of the mandible show shallow fossae for the attachments of portions of the jaw adductor musculature; however, the adductor fossa is elongate and deep. A pronounced prearticular process extends mediodorsally from the anteromedial edge of the articular surface of the mandible. The retroarticular process is dorsoventrally flattened; it curves in a semicircle around the quadratic articulation to lie ventromedial to the jaw joint. This medial displacement corresponds to the appearance of the external auditory meatus, which faces posterolaterally rather than laterally as in many other lizards.

The premaxillae, maxillae, and dentaries bear conical pleurodont teeth in a single row along the jaw margins; the palatines and pterygoids are edentulous. The teeth become large posteriorly along the tooth row. The largest teeth lie approximately in the posteriormost third to quarter of the tooth row whereas those teeth posterior to them are much smaller.

The aponeuroses

The jaw adductor musculature of *Trachydosaurus* is subdivided by extensive and complex systems of external and internal tendinous sheets. The aponeurotic pattern is best described under three headings. First is the coronoid aponeurosis, extending the areas of attachment for the major adductors on the lateral and medial aspects of the mandible. Next are the two aponeuroses (temporal fascia and quadrate aponeurosis) that extend the bony surfaces along the arcades of skull and quadrate from which these fibers originate. Finally, there are the three aponeuroses (pterygoid, internal pterygoid, and deep pterygoid) of the medially placed M. pterygoideus, which extend the areas of origin and insertion of this prominent muscular mass.
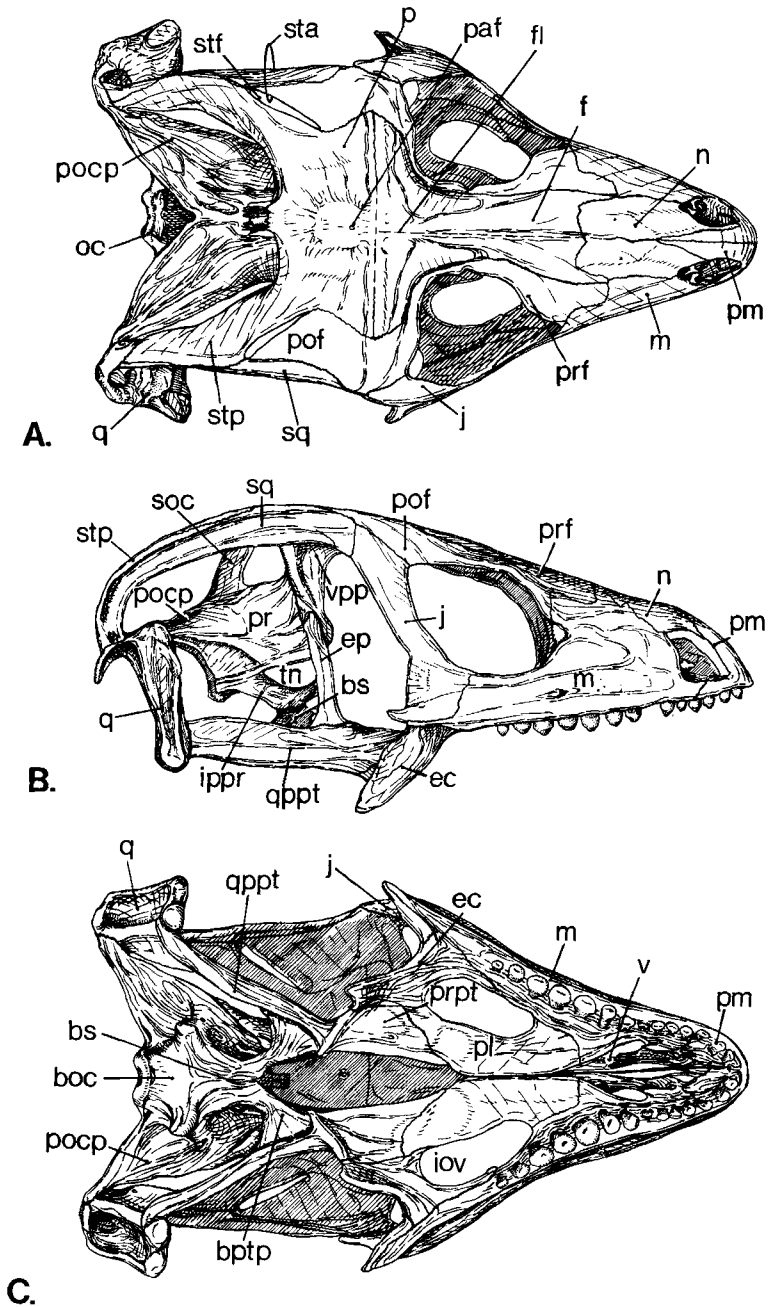
Fig. 1. *Trachydosaurus rugosus*. Dorsal (A, D), lateral (B, E), and ventral (C, F) views of the skull and mandible. af, adductor fossa; an, angular; ar, articular; as, articular surface; boc, basioccipital; bptp, basipterygoid process; bs, basisphenoid; cf, coronoid fossa; co, coronoid; cp, coronoid process; d, dentary; ec, ectopterygoid; ep, epipterygoid; f, frontal; fl, fusion line; iov, infraorbital vacuity; ippr, inferior process of prootic; j, jugal; m, maxilla; n, nasal; oc, occipital; p, parietal; paf, parietal foramen; parp, prearticular process; pl, palatine; pm, premaxilla; pocp, paraoccipital process; pof, postorbitofrontal; pr, prootic; prf, prefrontal; prpt, palatal ramus of pterygoid; q, quadrate; qppt, quadrate process of pterygoid; rap, retroarticular process; san, surangular; soc, supraoccipital; sq, squamosal; sta, supratemporal arch; stf, supratemporal fossa; stp, supratemporal process; tn, trigeminal notch; v, vomer; vpp, ventral process of parietal.
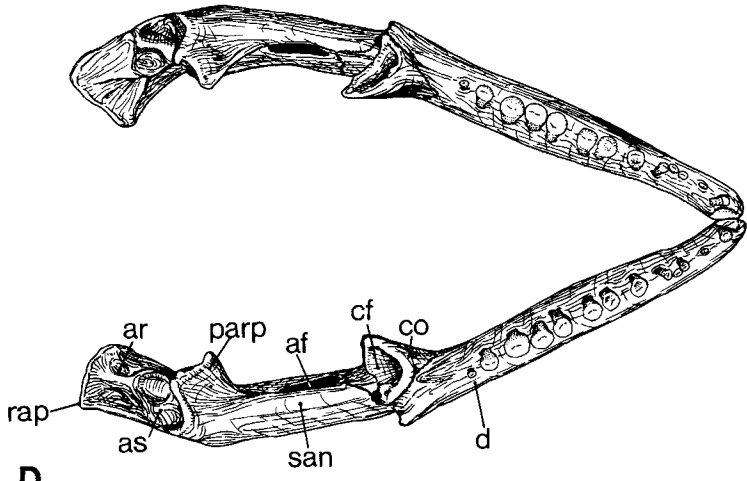
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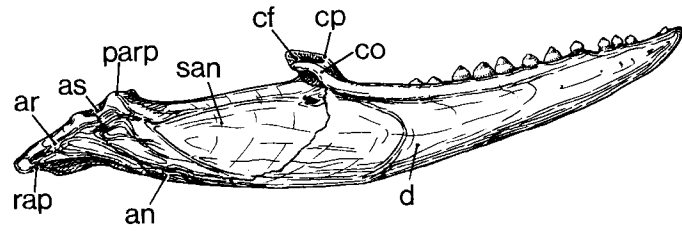
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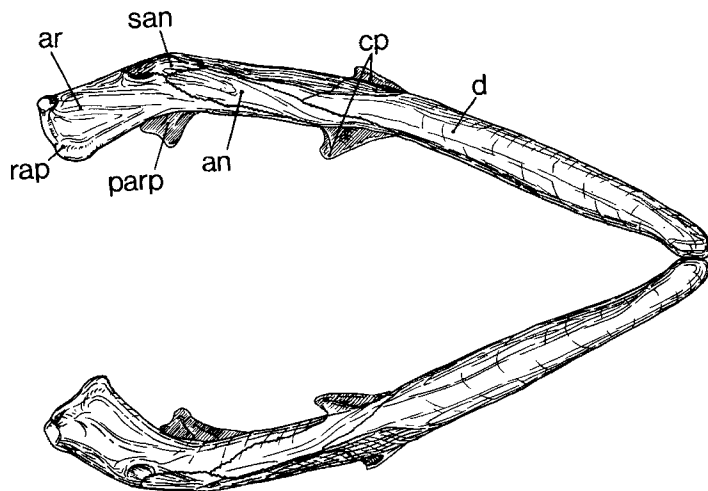
F.

Despite their characteristic locations, these sheets show substantial variation in their length and thickness. Commonly, one sees short diverticula extending at right angles from the aponeurotic plates. Also, some shorter and less obvious aponeuroses arise among the major ones; for instance, a short sheet (va, Fig. 6A) that arises from the posterodorsal mandibular surface and interdigitates between the medial and lateral plates of the quadrate aponeurosis. The extent of such "irregularities" obviously affects the actual length of muscle fibers and thus their length-tension relation. Consequently, these lengths must be determined specifically for each muscle.

An enormous, scroll-like coronoid aponeurosis arises from the coronoid portion of the mandible and curves around and through the external and internal adductor musculature to lie interspersed among the tendinous sheets descending from elements of the skull. For purposes of description, this coronoid aponeurosis is here divided into five connected parts. This description differs somewhat from that of Gomes ('74), as her two-dimensional scheme is difficult to correlate with functional subdivisions of the adductor muscles; our description is also more complex than the scheme of Rieppel ('81).

Part I of the coronoid aponeurosis (2, aponévrose superficielle: Gomes, '74; ventrally deflected lateral sheet of the Bodenaponeurosis: Rieppel, '81) is the most lateral division and is aligned mainly in an anteroposterior (parasagittal) plane. When the skin is removed, a triangular area of the posterior edge of part I (Ip, Figs. 2B, 10C) may be exposed on the posterolateral surface of the adductor mass, dorsal to the quadratojugal ligament. However, most of the lateral surface of the anterodorsal portion of part I (Ia, Figs. 4, 10C) lies deep to muscle (MAME-2) that reaches it from the temporal fascia. Part I continues ventrally beneath the quadratojugal ligament as a superficial, dense aponeurotic sheet (Iv, Fig 2) (ventral aponeurosis of M. adductor mandibulae externus superficialis, Haas, '73); it extends anteriorly to the level of the eye to form a deep pocket that covers the muscle on the lateral face of the mandible, to which it attaches along the periphery of the muscle (MAME-1).

Part II (3, aponévrose ap2, coronoïde: Gomes, '74; lateral septum of the Bodenaponeurosis: Rieppel, '81) continues the anterior edge of part I and curves medially and deeply with its fibers ascending at a posteriorly di-

rected angle of close to 45° toward the dorsum of the quadrate (Figs. 4, 5, 10). Anteriorly, its fibers arise from and lie parallel to the surface of the lateral, shelflike portion of the coronoid process and the posterior lip of the cupped fossa at the apex of the coronoid process. The upper region of the anteriorly convex part II gives rise to a parasagitally aligned posterodorsally extending wing (part IIA, Fig. 4). Thus, a horizontal section, some distance dorsal to the mandible, would show the sheet to be triradiate. The medial edge of part II descends toward the coronoid tip and only the base is continuous with parts III and IV (Figs. 5, 6B, 10).

Part III (not explicitly described by Gomes or Rieppel) turns posteriorly from the medial edge of Part II (Figs. 6B, 10). Part III is a vertically aligned sheet that extends posterodorsally and medially across the lower third of the infratemporal fossa toward the paraoccipital process. This aponeurosis has an extensive, arclike attachment from the medial base of Part II, from the posterior side of the base of the medial coronoid ridge, and from the inferior lip of the length of the adductor fossa.

Part IV (4, aponévrose du fond, coronoïde: Gomes, '74; "the" Bodenaponeurosis: Rieppel, '81) turns anteriorly from the medial base of part II (Figs. 5, 10). Its basal fibers attach onto the anteromedial edge of the coronoid cup and lie in almost a parasagittal plane. The tendon strap extends dorsoposteriorly and medially through the center of the posttemporal fossa and rotates such that its distal end lies in a horizontal plane. Therefore, the basal portion of part IV presents lateral and medial faces, whereas the distal portion has dorsal and ventral faces. In dorsal view, the free end of part IV lies medial to the supratemporal process of the parietal and squamosal.

Part V (5, aponévrose du muscle pseud. superf.: Gomes, '74; anterior expansion of the Bodenaponeurosis: Rieppel, '81) curves medially and then posteriorly from the medial side (not the free edge) of part IV (Figs. 5, 6, 10). It attaches along the length of the crest of the medial coronoid ridge and extends dorsal to the apex of the coronoid process. Part V is aligned in an almost directly vertical plane; it billows in an anteriorly concave pattern, has a free medial edge, and delineates the musculature versus the buccal cavity.

Two separate aponeuroses provide areas of origin for portions of the external adductor muscles. Most externally, a thin sheet of con-
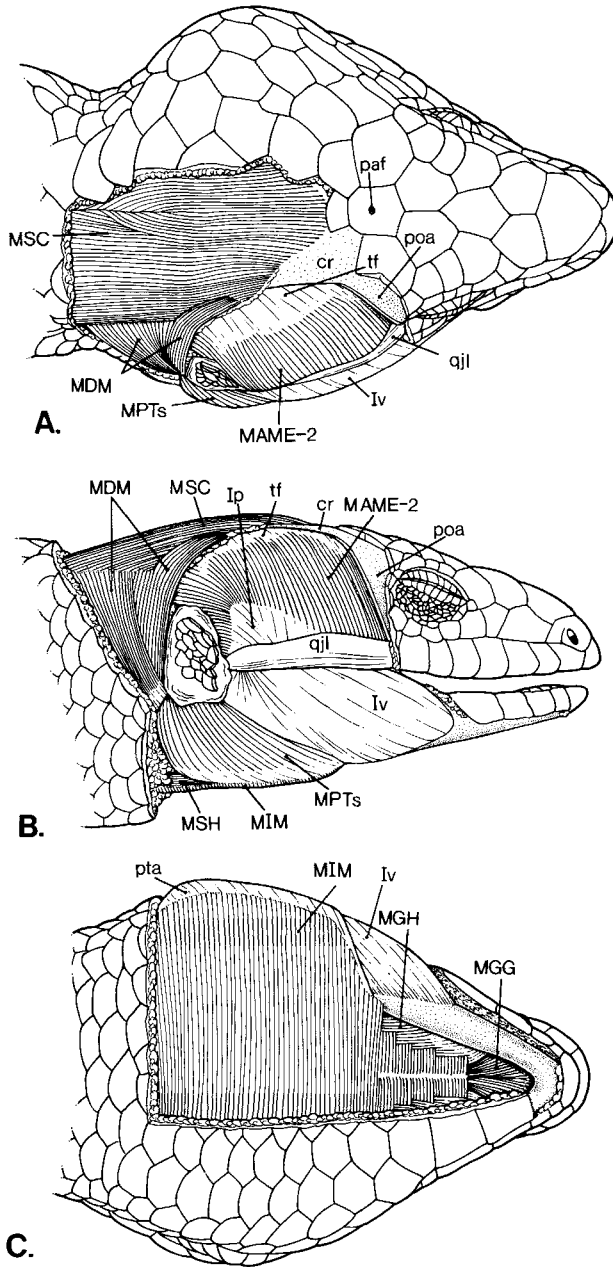
Fig. 2. *Trachydosaurus rugosus*. Dorsal, lateral, and ventral views of dissection after removal of osteoderms, skin, and connective tissue. Note that the MAME-2 extends anteriorly, deep to the postorbital arch, and the temporal fascia attaches to the margin of the cranial roof. cr, cranial roof; Ip, coronoid aponeurosis, part Ip; Iv, coronoid aponeurosis, part Iv; MAME-2, M. adductor mandibulae externus, part 2; MDM, M. depressor mandibulae; MGG, M. genioglossus; MGH, M. geniohyoideus; MIM, M. intermandibularis; MPTs, M. pterygoideus superficialis; MSC, M. spinalis capitis; MSH, M. sternohyoideus; paf, parietal fossa; poa, postorbital arch; pta, pterygoid aponeurosis; qjl, quadratojugal ligament; tf, temporal fascia.

nective tissues lies immediately deep to the dorsal integument as a cover of the temporal fossa (tf, Fig. 2). This "temporal fascia" (Rieppel, '81) (1, aponévrose superficielle: Gomes, '74; dorsal aponeurosis: Haas, '73; Decksehne: Poglayen-Neuwall, '54) spans the zone along the dorsolateral crest of the supratemporal process and the dorsal aspect of the squamosal to extend laterally and ventrally for approximately 1 cm; it forms a dorsolateral roof of the adductor mass. The "quadrate aponeurosis" (Rieppel, '81) (aponévrose apl: Gomes, '74) is heavier, lies deeper, and has three parts (Figs. 5, 6, 10). A relatively small lateral wing (not illustrated) originates from the dorsal angle of the quadratic attachment of the two deeper plates. This wing extends dorsally, laterally, and anteriorly as a fan-shaped array of radiating fibers. A lateral plate originates from the large, knoblike protrusion of the anterodorsal head of the quadrate and descends anteroventrally and laterally as a sheet roughly parallel to part I of the coronoid aponeurosis. The fibers of this aponeurosis are aligned at approximately 40° from the horizontal and descend along the lateral aspect of the mandible (but do not attach to it) to enter the pocket formed by part Iv of the coronoid aponeurosis. A medial plate originates deep to the origin of the lateral plate along the median edge of the quadrate knob. This second tendon descends inward from the lateral plate but is shorter, narrower, and more medially directed. It terminates slightly dorsal to the dorsomedial edge of the mandible. The two plates of the quadrate aponeurosis are dorsally continuous for nearly the length of the medial plate, thus forming an inverted v-shaped cup over the mandible.

Three aponeuroses provide attachment of the enormous mass of the M. pterygoideus: 1) the pterygoid aponeurosis, forming a superficial ventral cover of the muscle, 2) the internal pterygoid aponeurosis, which subdivides the muscle into superficial and deep parts, and 3) the deep pterygoid aponeurosis, which forms part of the deep floor of the muscle (Fig. 7). The large, fan-shaped pterygoid aponeurosis originates from the posterior edge of the palatal ramus of the pterygoid and the posteroventral edge of the ectopterygoid. Its most medial fibers pass posteromedially; the lateral fibers of the sheet take a sharp posterolateral course superficial to the relatively flattened posteroventral aspect of the mandible (to which they do not connect). The stout internal pterygoid aponeurosis extends anteromedially from the curved medial edge of the posterior portion of the mandible, thus serving as an extension of the insertion area of the ventral bladelike surface. The deep pterygoid aponeurosis attaches to the posteromedial edge of the palatal ramus of the pterygoid and along the anterior two-thirds of the ventral edge of the quadrate ramus of the pterygoid. Aponeurotic fibers radiate posteromedially and posterolaterally off the quadrate ramus, thus giving the deep pterygoid aponeurosis an elongate, leaflike form.

TOPOGRAPHIC DESCRIPTION
Side and top of head

The entire head and body of *Trachydosaurus* are covered with a dense coat of thick osteodermal scales. This mass (more than 1 mm thick in adults) is very firmly adherent to the top of the skull down to a line slightly ventral to the dorsal edge of the maxilla, as well as from the tip of the premaxilla to the middle of the parietal. Thus, there is almost no flexibility in the preorbital and orbital regions. Only the eyelids are flexible, but their integument is extremely thick as well. The attachment of the row of labial osteoderms is somewhat looser along the length of the maxilla and premaxilla. Therefore, stiff, relatively immobile skin covers the dorsal surface of the head back to the level of the ear, beyond which the neck narrows markedly, and its osteoderms assume overlapping rather than butt junctions. Whereas this cranial covering may be deformed slightly it permits only minimal flexibility; the covering of the trunk allows greater mobility.

Posterior to the jugal (postorbital) arch, in the expanse of the infratemporal fossa, the integument bulges more widely away from the underlying musculature and the interscalar butt sutures show some flexibility. Particularly, the posterior extension of the labial fold overlying the quadratojʋgal ligament is 1–2 mm removed from the muscle surface in adult animals, a gap that may be more than 3 mm wide just anterior to the ear. Removal of integument from the lateral postorbital aspect of the head discloses a heavy fat pad which covers the posterior half of the infratemporal fossa. Whereas the dorsal integument is tightly connected to the cranial roof, the supratemporal process is deeply inserted within the adductor muscle masses and the integument here is variably attached by tendons arising from the surface of and deep within these. Posterior to the

parietal plate and supratemporal process, the integument lies fairly closely over the neck musculature. There is relatively little fatty space between it and the muscles of the spinalis capitis complex.

Almost one-third of the mass of the head is occupied by the mandibular adductor system. These muscles extend anteriorly deep to the postorbital arch (which has to be broken to visualize them, Fig. 3), dorsally up to the deep surface of the cranial roof, and medially to the braincase. Their medial limit is best visualized by removing the M. spinalis capitis (attaching to the skull between the supratemporal processes of the parietal and to the occipital region) and the lateral part of the cranial roof (Figs. 3, 4). The adductor musculature runs from the cranial roof, from the braincase, and from the dorsal and anterior portions of the quadrate to insert variously on the mandible.

The back of the head and neck are overlain by the relatively thin sheet of the M. constrictor colli which reaches from a dorsal fascia, in part continuous with the integument, to cross the throat ventral to the articulation of the lower jaw. Once this muscle is pulled aside, the small, bipartite M. depressor mandibulae is exposed (Fig. 2).

The stout quadratojugal ligament extends from the posterolateral margin of the quadrate up to the lateroventral tip of the jugal (Fig. 2). Part I of the coronoid aponeurosis, and the adductor mass it covers, pass deep to it to continue ventrally along the lateral aspect of the mandible. A ridge of unarmored tissue forms along the dorsomedial edge of the ligament to provide insertion for a very thin layer of superficial muscle fibers. More posteriorly lies the posterolateral aspect of the M. pterygoideus which attaches to the posteroventral aspects of the mandible and then swings medially toward its origin on the floor of the skull.

Whenever the lizard gapes, the labial edges and their posterior extensions separate. The angulus oris is posteriorly prolonged past the coronoid region so that the side and front of the adductor mass are exposed during the gape. The surface of the lateral rictal plate (Mundplatt) is then covered by a thin dense membrane (Fig. 3).

Ventral surface

The osteoderms overlying the mandibular area have butt joints, whereas the postmandibular ones take on overlapping junctions. Overall, the integument lies much further from the bones of the ventral than of the dorsal jaw. On its removal, one sees a layer of adipose tissue lateral to the mandible. In the intermandibular zone, the integument lies some distance from the underlying muscles, except in regions where muscular slips attach directly or via tendinous integumentary insertions.

The skin is connected to the mandibles by dense tendinous sheets at and immediately posterolateral to the symphysial region and via a wider and more flexible sheet of connective tissues more posteriorly. Near the angulus oris, the skin becomes attached to the quadratojugal ligament and this is loosely connected to part Ip of the coronoid aponeurosis; thus, there is some independence between the integument and the posterior portion of the mandible as the animal gapes. Although the integumentary plate can bend, it shows little capacity for longitudinal deformation anterior to the gular region. An intermediate strip of fatty tissue lies within the fold of skin along the back of the jaw and extends anteriorly parallel to the mandible.

A series of tendinous slips connects the symphysial region to the skin at approximately the level of the first paired chin shields where this mass of oriented collagen is attached for the length of two scales. More posteriorly, it continues as a second tendon that provides insertion for the midventral portion of the mandibulohyoideus muscles. Superficially, the mandibulohyoideus musculature is covered by the extremely thin and transversely oriented M. intermandibularis (Fig. 2C). As noted in Haas ('73), the fibers of the M. geniohyoideus (MGH, Figs. 2–4) do not reach the symphysis, the posterior displacement of their medial tips apparently having proceeded by a transformation into tendon with part of this attached to the skin. Once the mandibulohyoid muscles are removed, the M. pterygoideus becomes the most obvious muscle in posterolateral and ventral views.

Tongue

Trachydosaurus possesses a large tongue that covers the floor of the oral cavity. The deep blue-purple color of the tongue creates a striking contrast to the pink and red hues of the oral lining. The leaflike tongue is widest posteriorly and tapers to a pointed tip; it is dorsoventrally flattened and has thin free edges. The very tip of the tongue is slightly expanded and bears a shallow midline cleft, thus giving the appearance of a broken ar-
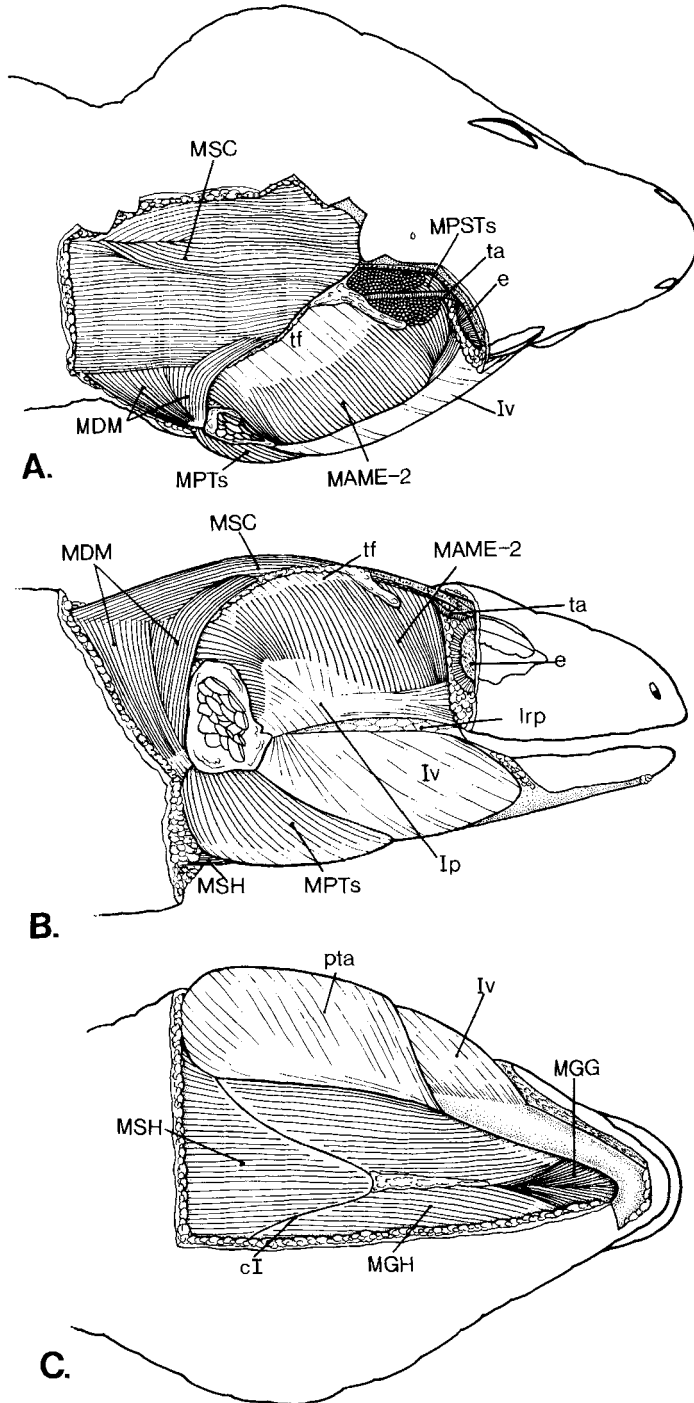
Fig. 3. *Trachydosaurus rugosus*. Dorsal, lateral, and ventral views of dissection after removal of the postorbital arch, lateral portion of the cranial roof, quadratojugal ligament, and the MIM. Note the anterior extent of the MAME-2 and the former attachments of the MAME-2 and MPSTs to the ventral side of the cranial roof. cI, (inscription over) ceratobranchial I; e, eye; Ip, coronoid aponeurosis, part Ip; Iv, coronoid aponeurosis, part Iv; lrp, lateral rictal plate; MAME-2, M. adductor mandibulae externus, part 2; MDM, M. depressor mandibulae; MGG, M. genioglossus; MGH, M. geniohyoideus; MPSTs, M. pseudotemporalis superficialis; MPTs, M. pterygoideus superficialis; MSC, M. spinalis capitis; MSH, M. sternohyoideus; pta, pterygoid aponeurosis; ta, temporal artery; tf, temporal fascia.
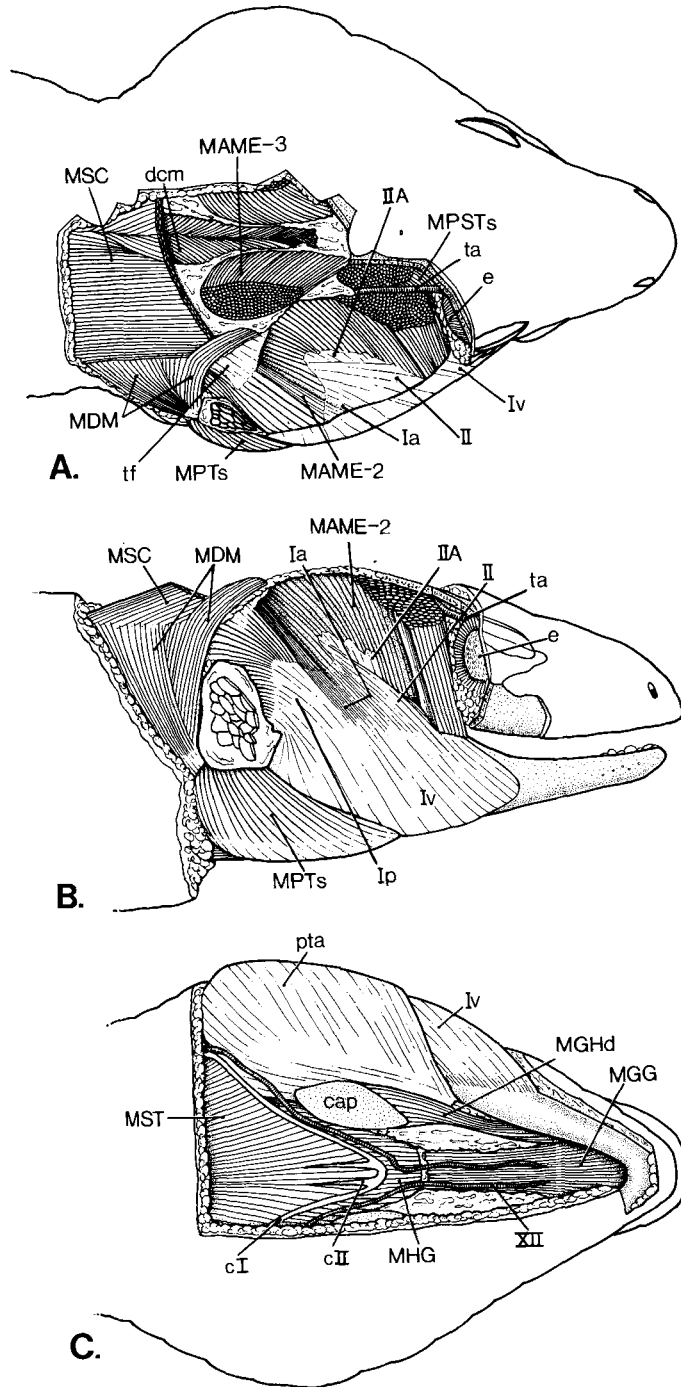
Fig. 4. *Trachydosaurus rugosus*. Dorsal, lateral, and ventral views of dissection after removal of parts of the MAME-2, MSC, MGH, and the MSH. Note that parts Ip, Ia, and II of the coronoid aponeurosis are regions of a continuous sheet of tendon that curves deeply into the external adductor; these are also contiguous with part Iv. cap, cartilage plate; cI, ceratobranchial I; cII, ceratobranchial II; dcm, deep cervical muscles; e, eye; Ia, coronoid aponeurosis, part Ia; II, coronoid aponeurosis, part II; IIA, coronoid aponeurosis, part IIA; Ip, coronoid apo-neurosis, part Ip; Iv, coronoid aponeurosis, part Iv; MAME-2, M. adductor mandibulae externus, part 2; MAME-3, M. adductor mandibulae externus, part 3; MDM, M. depressor mandibulae; MGG, M. genioglossus; MGHd, deep slip of M. geniohyoideus; MHG, M. hyo-glossus; MPSTs, M. pseudotemporalis superficialis; MPTs, M. pterygoideus superficialis; MSC, M. spinalis capitis; MST, M. sternothyroideus; pta, pterygoid apo-neurosis; ta, temporal artery; tf, temporal fascia; XII, ramus lingualis of hypoglossal nerve.

rowhead. The entire dorsum of the tongue is covered with small, soft, scalelike papillae, the most posterior ones of which are larger than the anterior ones. The papillae continue around the slightly serrate edges of the tongue toward its base, near which the surface becomes smooth and membranous. A frenulum extends sagittally from the mandibular symphysis to the ventral surface of the tongue, leaving only the anterior half of the tongue free. The glottis lies on the midline immediately posterior to the lingual base.

MUSCULATURE
Nomenclature

The cranial musculature of *Trachydosaurus rugosus* (Table 1) has been only partially described (Camp, '23; Poglayen-Neuwall, '54); that of the closely related species *Tiliqua scincoides* has been given more thorough attention (Lakjer, '26; Poglayen-Neuwall, '54; see Haas, '73, for a brief review). Recently, the jaw adductor musculature of some specialized, burrowing scincomorph lizards has also been described (Rieppel, '81). The present description of muscles follows the general scheme of Haas ('73). However, the accounts of muscular subdivisions differ as they are to serve as the bases of functional hypotheses.

In *Trachydosaurus*, the jaw adductor musculature is massive and complex whereas the Mm. intermandibularis and depressor mandibulae and the muscles of the constrictor internus dorsalis complex are relatively simple. The mandibular adductors have traditionally been subdivided into external, internal, and posterior portions (each of which could in turn be further subdivided) and defined by the nature of their attachment to the major aponeuroses and location relative to the major branches of the trigeminal nerve (Haas, '73). Here, the external and internal adductor masses are easily discerned from one another by their respective positions lateral and medial to the maxillary and mandibular divisions of the trigeminal nerve. Additionally, subdivision of the internal adductor into traditional pseudotemporalis and pterygoideus muscles presents no problem, as the pterygoideus forms the large muscular ball at the posterior corner of the jaw and the pseudotemporalis lies anteromedially to the main adductor mass. However, subdivision of the external adductor and recognition of the posterior adductor along traditional lines is more difficult because of the unique form of the coronoid aponeurosis. The external adductor is divided into four major parts, or "muscles," by parts I–IV of the coronoid aponeurosis. For purposes of description, these muscles are here termed M. adductor mandibulae externus, parts 1 through 4. There is no clearly defined posterior adductor.

The adductor complex
M. adductor mandibulae externus—general

The M. adductor mandibulae externus lies lateral to the maxillary and mandibular divisions of the trigeminal nerve and is divided into four parts, 1, 2, 3, and 4. Part 1 is the posteroventral and lateral unit, part 2 is the anterior component, part 3 is the dorsomedial one, and part 4 is the deep unit. Each part is bounded and defined by certain parts of the coronoid aponeurosis.

M. adductor mandibulae externus, part 1 (MAME-1, Figs. 5, 6, 9, 10)

The M. adductor mandibulae externus, part 1, is a large, multipinnate, posteroventrally situated unit of the external adductor; it is

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TABLE 1. List of major jaw muscles

I.   M. adductor mandibulae externus
    A. M. adductor mandibulae externus, part 1 (MAME-1)
    B. M. adductor mandibulae externus, part 2 (MAME-2)
    C. M. adductor mandibulae externus, part 3 (MAME-3)
    D. M. adductor mandibulae externus, part 4 (MAME-4)
II. M. adductor mandibulae internus
    A. M. pseudotemporalis
        1. M. pseudotemporalis superficialis (MPSTs)
        2. M. pseudotemporalis profundus (MPSTp)
    B. M. pterygoideus
        1. M. pterygoideus superficialis (MPTs)
        2. M. pterygoideus profundus (MPTp)
III. Constrictor internus dorsalis
    A. M. protractor pterygoidei (MPPT)
    B. M. levator pterygoidei (MLPT)
    C. M. levator bulbi ventralis (MLBV)
IV. M. depressor mandibulae (MDM)
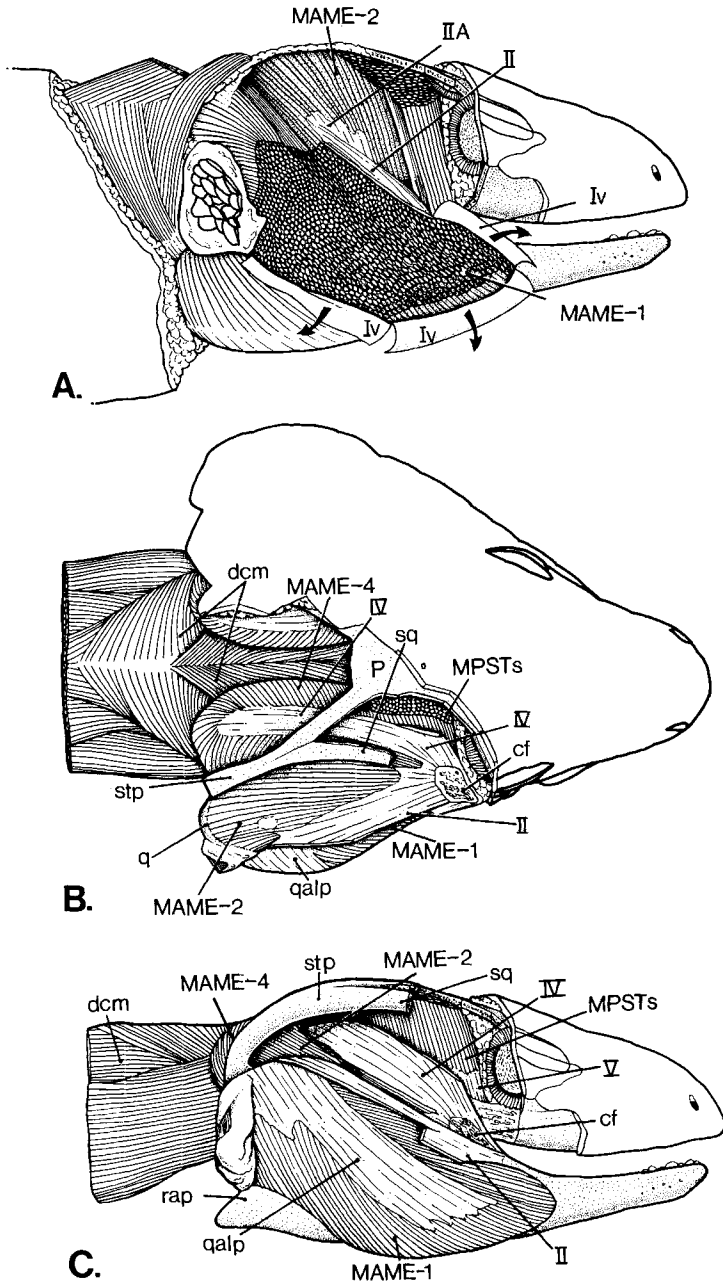V.   M. intermandibularis (MIM)

Fig. 5. *Trachydosaurus rugosus.* A. Lateral view of dissection after reflecting part I of the coronoid aponeurosis, showing the attachment of the MAME-1 to its medial (deep) surface. B, C. Dorsal and lateral views after removal of the MSC, MDM, MPTs, MAME-3, most of the MAME-2, and lateralmost portion of the MAME-1. Note that parts II and IV of the coronoid aponeurosis are contiguous sheets; also note the extent of part IV and the lateral plate of the quadrate aponeurosis. cf, coronoid fossa; dcm, deep cervical muscles; Iv, coronoid aponeurosis, part Iv; II, coronoid aponeurosis, part II; IIA, coronoid aponeurosis, part IIA; IV, coronoid aponeurosis, part IV; MAME-1, M. adductor mandibulae externus, part 1; MAME-2, M. adductor mandibulae externus, part 2; MAME-4, M. adductor mandibulae externus, part 4; MPSTs, M. pseudotemporalis superficialis; P, parietal; q, quadrate; qalp, quadrate aponeurosis, lateral plate; rap, retroarticular process; sq, squamosal; stp, supratemporal process; V, coronoid aponeurosis, part V.
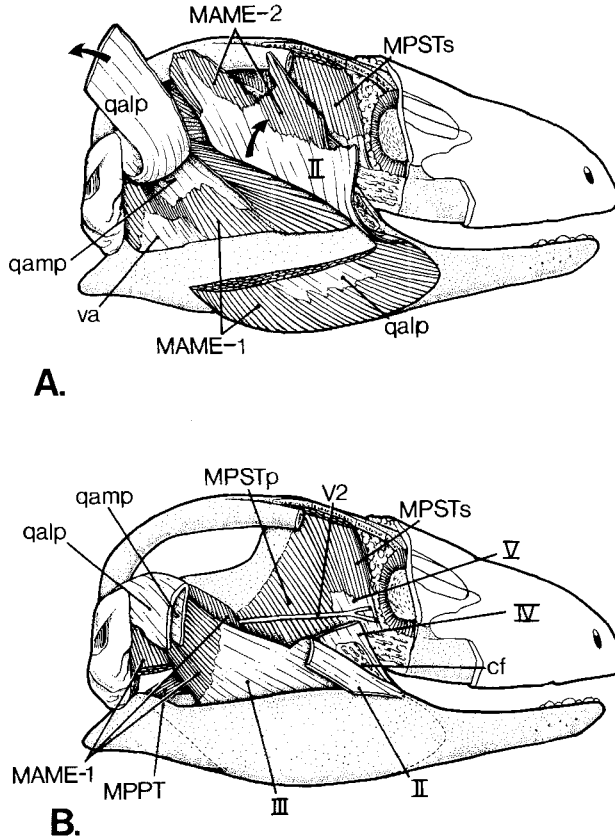
Fig. 6. *Trachydosaurus rugosus*. Lateral views of dissection. In A, the dorsolateral part of the MAME-1 has been removed and the quadrate aponeurosis and part II of the coronoid aponeurosis reflected to show the deeper portion of the MAME-1. In B, the MAME-2, MAME-4, and all but the deepest part of the MAME-1 have been removed. Note that parts II, III, and IV of the coronoid aponeurosis are contiguous, as are the two plates of the quadrate aponeurosis. Also note the relation of V2 to the MPSTs and MPSTp. cf, coronoid fossa; II, coronoid aponeurosis, part II; III, coronoid aponeurosis, part III; IV, coronoid aponeurosis, part IV; MAME-1, M. adductor mandibulae externus, part 1; MAME-2, M. adductor mandibular externus, part 2; MPPT, M. protractor pterygoidei; MPSTp, M. pseudotemporalis profundus; MPSTs, M. pseudotemporalis superficialis; qalp, quadrate aponeurosis, lateral plate; qamp, quadrate aponeurosis, medial plate; V, coronoid aponeurosis, part V; va, variable aponeurosis; V2, maxillary division of trigeminal nerve.

almost entirely enclosed by the hoodlike arrangement of parts I, II, and III of the coronoid aponeurosis. The MAME-1 originates from the anterior face of the quadrate, from the entirety of the quadrate aponeurosis, and from the posteroventral corner of the prootic. Muscle fibers radiate anteroventrally. Fibers arising from the lateral face of the quadrate and from the lateral wing and lateral side of the lateral plate of the quadrate aponeurosis insert onto the medial surfaces of parts Ip and Iv of the coronoid aponeurosis; those arising from the medial side of the lateral plate of the quadrate aponeurosis insert onto

the dorsal and lateral aspects of the mandible. Muscle fibers originating from the quadrate between the two plates of the quadrate aponeurosis and from the lateral side of the medial plate of the quadrate aponeurosis insert onto the dorsal and dorsomedial surfaces of the mandible from the prearticular process to the posterior side of the coronoid process. Fibers arising from the anterior edge and medial face of the medial plate of the quadrate aponeurosis and from the medial face of the quadrate insert onto the posterior side of part II of the coronoid aponeurosis, and onto the lateral face of part III. Fibers arising
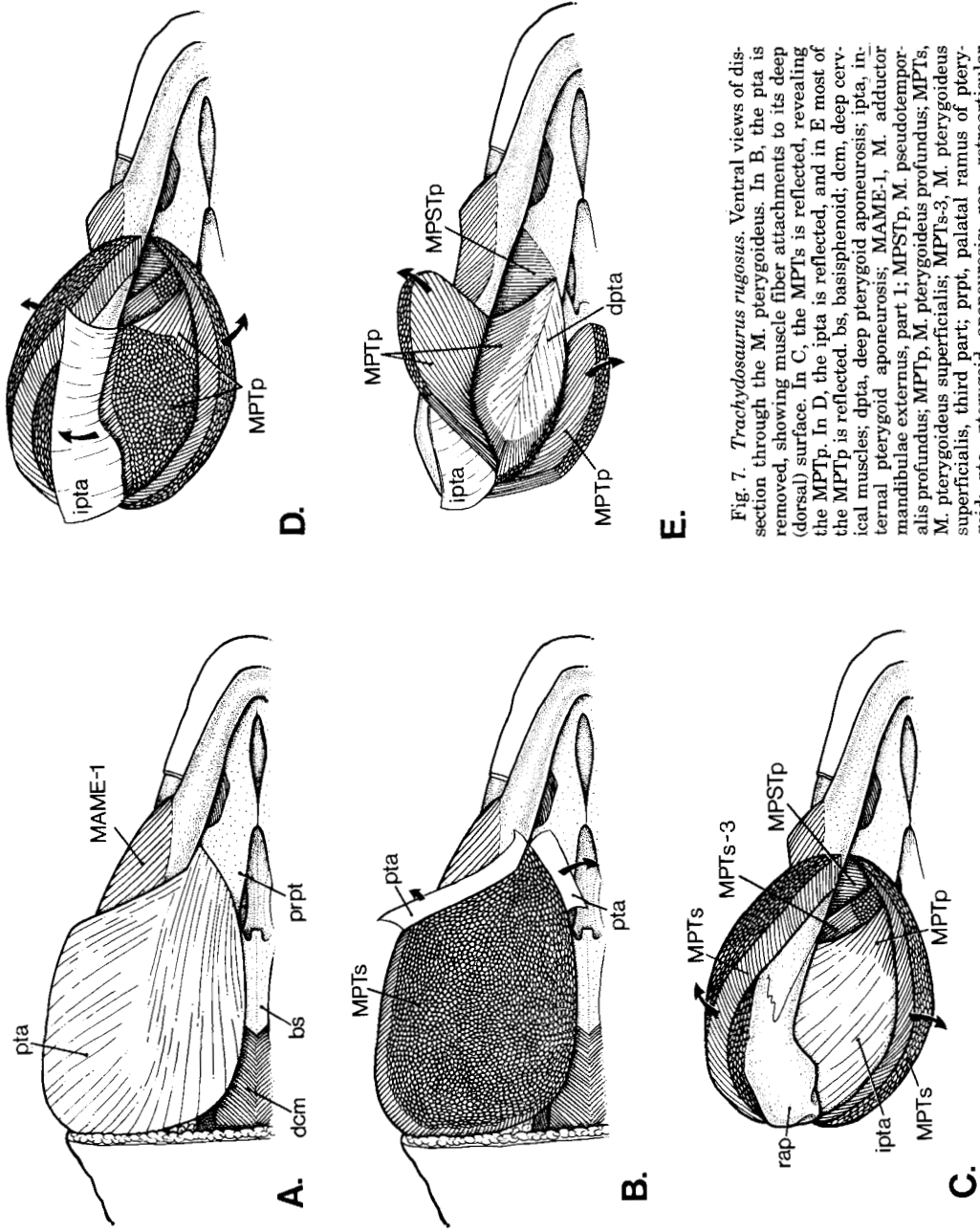
Fig. 7. *Trachydosaurus rugosus.* Ventral views of dissection through the M. pterygoideus. In B, the pta is removed, showing muscle fiber attachments to its deep (dorsal) surface. In C, the MPTs is reflected, revealing the MPTp. In D, the ipta is reflected, and in E most of the MPTp is reflected. bs, basisphenoid; dcm, deep cervical muscles; dpta, deep pterygoid aponeurosis; ipta, internal pterygoid aponeurosis; MAME-1, M. adductor mandibulae externus, part 1; MPSTp, M. pseudotemporalis profundus; MPTp, M. pterygoideus profundus; MPTs, M. pterygoideus superficialis; MPTs-3, M. pterygoideus superficialis, third part; prpt, palatal ramus of pterygoid; pta, pterygoid aponeurosis; rap, retroarticular process.

from the posteroventral corner of the prootic insert onto the dorsoposterior portion of the medial face of part III of the coronoid aponeurosis. The prootic portion of the MAME-1 lies posterolateral to the mandibular division of the trigeminal nerve, which separates the MAME-1 from the M. pseudotemporalis profundus. Muscle fibers measure 10 mm for the lateral and intermediate deep and 5–8 mm for the lateral and medial deep portions.

M. adductor mandibulae externus, part 2 (MAME-2, Figs. 2–5, 9, 10)

The M. adductor mandibulae externus, part 2, is the anterodorsal component of the external adductor. It inserts onto the lateral face of part Ia of the coronoid aponeurosis, onto the anterior face of part II, onto the entirety of part IIA, onto the lateral face of part IV, and directly into the cupped fossa of the coronoid process. Thus, the muscle is in essence "focussed" onto the coronoid process. The area of origin is extensive as well. Muscle fibers arise from the deep surface of the temporal fascia, from the deep, superior end of the jugal, from the deep lateral half of the postorbitofrontal, from the lateral and medial sides and inferior edge of the length of the squamosal, from a small tendinous wing that extends anteroventrally off the ventral edge of the posterior squamosal, and from the dorsum of the quadrate. Angles and lengths of the fibers in this muscle change gradually from front to rear; those having a more anterior origin descend onto their tendons in a relatively straight vertical alignment, whereas those having a more posterior origin (particularly those from the quadrate) are more curved and more horizontal. The anterior fibers are approximately 16 mm long, whereas the posterior fibers measure approximately 8 mm. A very thin, most superficial layer of the anterior fibers of the MAME-2 (indistinguishable from it dorsally) inserts onto the dorsal and medial surfaces of the lateral rictal plate, rather than onto the coronoid aponeurosis. This slip of fibers extends from the angulus oris as far posteriorly as part Ip of the coronoid aponeurosis. Because of the bend of the coronoid aponeurosis at the junction of parts II and IV and the distal separation of those sheets, the MAME-2 appears to be discontinuous where its deeper fibers diverge slightly in passing to the appropriate tendon strap. The temporal artery crosses the dorsomedial edge of the muscle and marks the separation between the MAME-2 and the deeper lying M. pseudotemporalis superficialis.

M. adductor mandibulae externus, part 3 (MAME-3, Figs. 4, 9, 10)

The third part of the M. adductor mandibulae externus occupies a posteromedial and dorsal position within the muscle. This part is situated in the posttemporal fossa and can be best appreciated when viewed from the dorsal aspect. Muscle fibers arise from a superficial aponeurosis that covers the dorsolateral surface of the medially bulging mass and from the dorsomedial and deep surfaces of the supratemporal process of the parietal. The fibers along the posteromedial tip of the muscle converge on a line over the medial edge of part IV of the coronoid aponeurosis and then curve sharply to join it. Fibers run initially in an anteromedial direction, then quickly curve deeply and in an anterolateral direction to achieve the dorsal face of the distal end of part IV, which extends well into the posttemporal fossa. This part of the external adductor takes a pronounced mediolateral line of direction to the coronoid process. Muscle fiber lengths in the MAME-3 are approximately 10 mm, with MAME-IV located about 2 mm deep from the dorsal surface of the muscular mass.

M. adductor mandibulae externus, part 4 (MAME-4, Figs. 5, 9, 10)

The fourth part of the M. adductor mandibulae externus is defined by its attachment onto the medial face of part IV of the coronoid aponeurosis. Muscle fibers arise from most of the lateral surface of the prootic (not from the most anterior and posteroventral parts or from the inferior process), from the anterior and dorsal surfaces of the paraoccipital process, and from a cup-shaped, laterally concave sheet of connective tissue that forms a posteromedial wall between the MAME-4 and the cervical musculature attaching onto the posterior side of the paraoccipital process. Dorsal paraoccipital fibers at first run anteriorly and slightly medially, then quickly curve anterolaterally to attach onto the deep (inferior) face of the distal tendon strap. The other fibers take a more direct anterolateral course to the aponeurosis. As with the overlying MAME-3, the MAME-4 has a pronounced mediolateral component in its line of action on the coronoid process. Muscle fibers in the compartments of the MAME-4 measure 5–7 mm posteriorly and 7–10 mm anteriorly.

M. adductor mandibulae internus—general

The internal adductor complex is separated from the external adductors by the maxillary

and mandibular divisions of the trigeminal nerve. It consists of two well-defined gross muscles, the pseudotemporalis and the pterygoideus. Each of these muscles is in turn subdivided into superficial and deep parts.

M. pseudotemporalis superficialis (MPSTs, Figs. 3–6, 8–10)

The superficial part of the M. pseudotemporalis takes origin from the medial half of the deep surface of the postorbitofrontal, from the deep surface of the parietal anterior and lateral to the ventral process, and from the upper lateral part of that process. Muscle fibers proceed ventrally and slightly anteriorly and the whole muscle tapers as it descends. Approximately one-half to two-thirds down its length, the MPSTs inserts into the upper part of part V of the coronoid aponeurosis (dorsal to the coronoid process). This

tendon wraps around the anterior margin of the muscle. The posteroinferior part of the MPSTs is entirely fleshy and is not clearly separable from the fibers of the M. pseudotemporalis profundus. The temporal artery crosses the dorsolateral side of the MPSTs and the maxillary division of the trigeminal nerve crosses the lateral side of the muscle at approximately the musculotendinous transition area. These two structures mark the separation between the MPSTs and the overlying MAME-2. The fibers measure approximately 11 mm.

M. pseudotemporalis profundus (MPSTp, Figs. 6–10)

The deep part of the M. pseudotemporalis is located posteroinferior to the superficial part. Muscle fibers arise from the ventrolateral side of the ventral process of the parie-
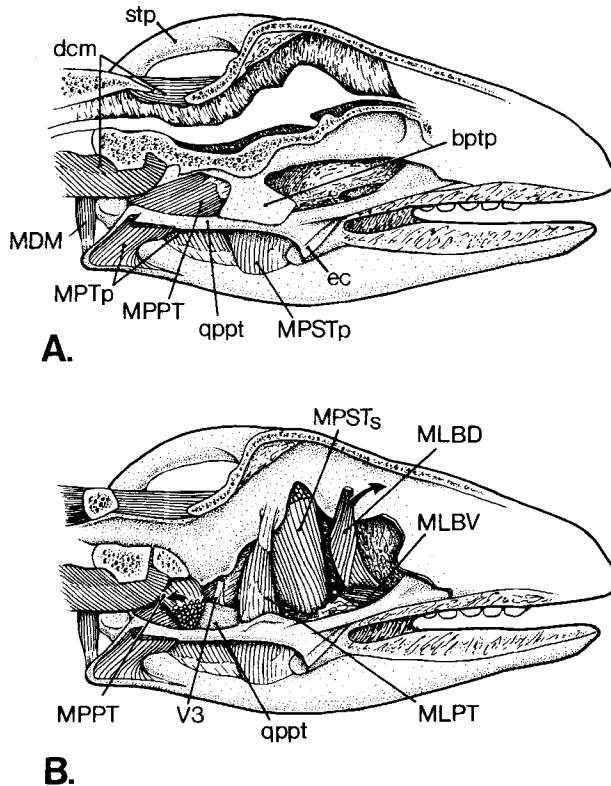

Fig. 8. *Trachydosaurus rugosus*. Medial view dissections showing the muscles of the constrictor internus dorsalis complex. In B, the bptp and neighboring bone are removed and the MPPT and MLBD reflected. bptp, basipterygoid process; dcm, deep cervical muscles; MDM, M. depressor mandibulae; ec, ectopterygoid; MLBD, M. levator bulbi dorsalis; MLBV, M. levator bulbi ventralis; MLPT, M. levator pterygoidei; MPPT, M. protractor pterygoidei; MPSTp, M. pseudotemporalis profundus; MPSTs, M. pseudotemporalis superficialis; MPTp, M. pterygoideus profundus; qppt, quadrate process of pterygoid; stp, supratemporal process; V3, mandibular division of trigeminal nerve.
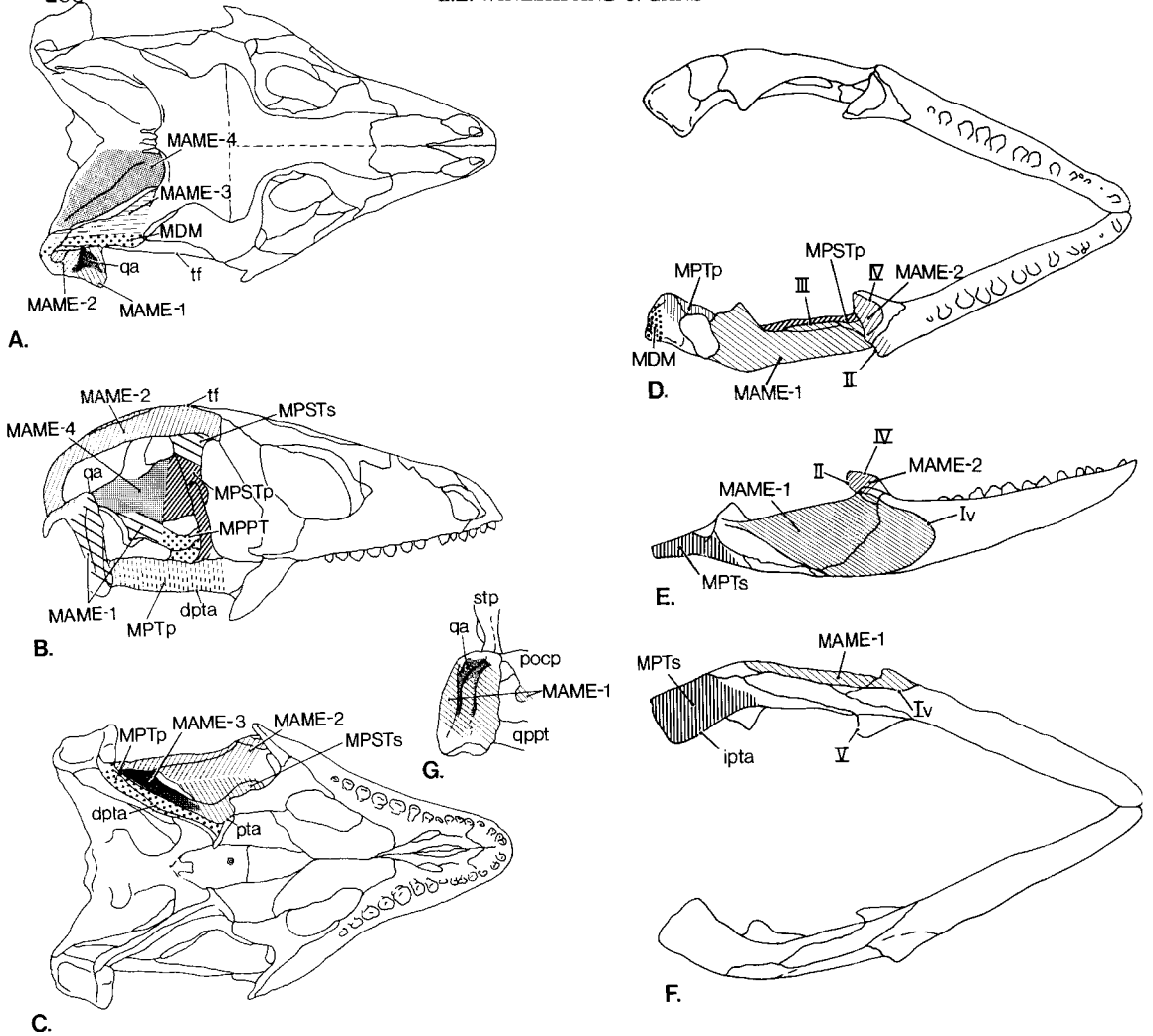
Fig. 9. *Trachydosaurus rugosus*. Dorsal (A, D), lateral (B, E), and ventral (C, F) views of skull and mandible with sites of attachment of cranial muscles and aponeuroses indicated. Frame G is an anterior view of the quadrate. dpta, deep pterygoid aponeurosis; II, coronoid aponeurosis, part II; III, coronoid aponeurosis, part III; ipta, internal pterygoid aponeurosis; IV, coronoid aponeurosis, part IV; Iv, coronoid aponeurosis, part Iv; MAME-1, M. adductor mandibulae externus, part 1; MAME-2, M. adductor mandibulae externus, part 2; MAME-3, M. adductor mandibulae externus, part 3; MAME-4, M. adductor mandibulae externus, part 4; MDM, M. depressor mandibulae; MPPT, M. protractor pterygoidei; MPSTp, M. pseudotemporalis profundus; MPSTs, M. pseudotemporalis superficialis; MPTp, M. pterygoideus profundus; MPTs, M. pterygoideus superficialis; pocp, paraoccipital process; pta, pterygoid aponeurosis; qa, quadrate aponeurosis; qppt, quadrate process of pterygoid; stp, supratemporal process; tf, temporal fascia; V, coronoid process, part V.

tal, from the anterolateral side of the prootic, from the anterior, lateral, and posterior sides of the epipterygoid, and from the lateral side of a small tendon located between the posterior edge of the epipterygoid and the mandibular division of the trigeminal nerve. The anterior muscle fibers travel anteroventrally and laterally and insert into the lower part of part V of the coronoid aponeurosis, inferior to the MPSTs. Most of the MPSTp fibers take a ventrolateral course, expand into a medially bulging muscle belly, and insert onto the inferior end of part V of the coronoid aponeurosis, onto the anterior and inferior portions of the medial face of part III of the coronoid aponeurosis, and onto the medioinferior edge
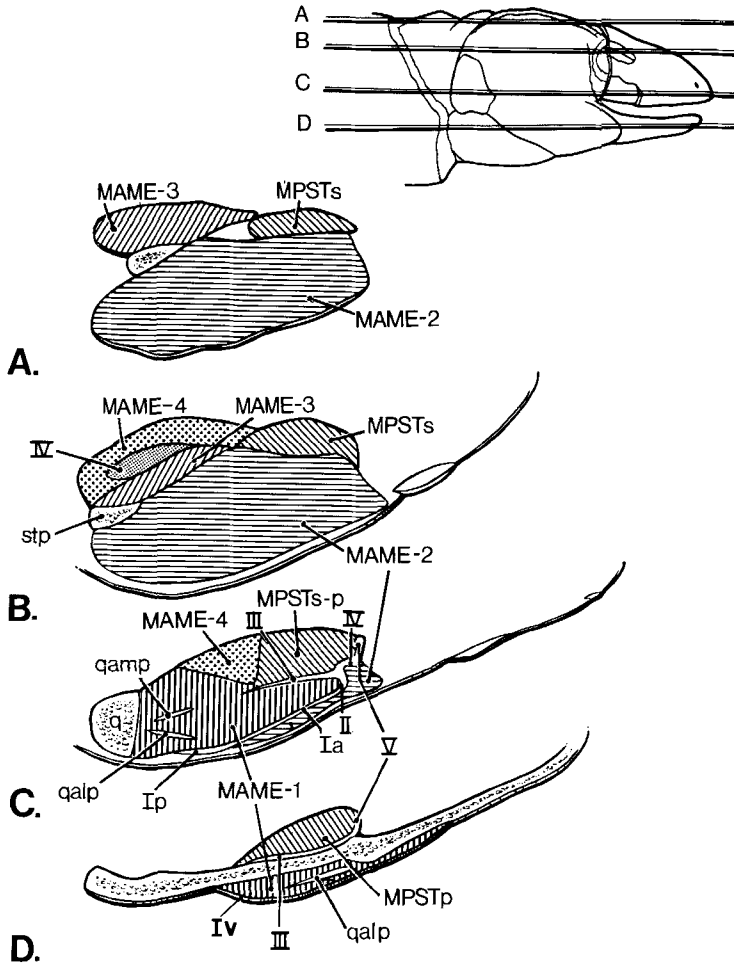
Fig. 10. *Trachydosaurus rugosus.* Schematic horizontal sections through the head showing the relationships of the coronoid aponeurosis to the adductor musculature. Section A is at the level of the cranial roof, B through the center of the posttemporal fossa, C at the coronoid process, and D through the body of the mandible. MAME-1, M. adductor mandibulae externus, part 1; MAME-2, M. adductor mandibulae externus, part 2; MAME-3, M. adductor mandibulae externus, part 3; MAME-4, M. adductor mandibulae externus, part 4; MPSTp, M. pseudotemporalis profundus; MPSTs, M. pseudotemporalis superficialis; qalp, quadrate aponeurosis, lateral plate; qamp, quadrate aponeurosis, medial plate; stp, supratemporal process; Ia, coronoid aponeurosis, part Ia; Ip, coronoid aponeurosis, part Ip; II, coronoid aponeurosis, part II; III, coronoid aponeurosis, part III; IV, coronoid aponeurosis, part IV; V, coronoid aponeurosis, part V.

of the mandible just inferior to the attachment of part III. The midlateral belly of the MPSTp is crossed by the maxillary division of the trigeminal nerve. The fibers measure approximately 12 mm.

M. pterygoideus superficialis (MPTs, Figs. 2–5, 7, 9)

The superficial M. pterygoideus forms the large, cushionlike ball of muscle located at the posterior end of the jaw. It is separated from the deep pterygoideus by the stout internal pterygoid aponeurosis. The ventral surface and medial curvature of the MPTs lie deep to the pterygoid aponeurosis. Muscle fibers arise from the deep side of the aponeurosis and from its origin along the posterior edge of the palatal ramus of the pterygoid and the posteroventral edge of the ectopterygoid. Near the bony edge the fibers of the superficial and deep pterygoid are indistinguishable.

The medial portion of the MPTs forms a tremendous belly. Its component fibers curve posterolaterally from their origin on the pterygoid aponeurosis to their insertion on the ventral face of the internal pterygoid aponeurosis as well as the medioventral aspect of the retroarticular process. The lateral portion of the MPTs passes posterolaterally from the pterygoid aponeurosis, to overlap the angular and the posterolateral end of the surangular. However, its fibers do not attach to these elements but curve to insert onto the lateroventral aspect of the retroarticular process. A third, small portion of the MPTs (MPTs-3, Fig. 7) originates from the pterygoid aponeurosis and the ectopterygoid and runs posterolaterally to insert onto the anterior edge of the internal pterygoid aponeurosis and to the medial edge of the mandible immediately anterior to that tendon. The fibers of the MPTs measure approximately 9 mm.

M. pterygoideus profundus (MPTp, Figs. 7–9)

The deep M. pterygoideus forms a deeper layer of the pterygoideus. Its fibers originate from a very dense tendon on the posterior edge of the palatal ramus of the pterygoid, from the entire ventral face, medial and lateral edges, and dorsal side of the lateral half of the deep pterygoid aponeurosis, from the lateral side of the length of the quadrate ramus of the pterygoid, and from the ventral and ventromedial sides of the distal third of the quadrate ramus of the pterygoid. Muscle fibers arising from the palatal ramus of the pterygoid and from the ventral face and medial edge of the deep pterygoid aponeurosis curve posterolaterally to insert onto the deep (dorsal) surface of the internal pterygoid aponeurosis. Muscle fibers arising from the lateral edge and dorsal face of the deep pterygoid aponeurosis and from the quadrate ramus extend posterolaterally to insert directly onto the posteromedial aspect of the mandible inferior to the attachment of the MAME-1 and onto the dorsomedial side of the retroarticular process, anterior to the insertion of the M. depressor mandibulae. The fibers of the MPTp measure approximately 6–8 mm.

Constrictor internus dorsalis complex—general

The muscles of the constrictor internus dorsalis complex link the braincase with the pterygoid and the lower eyelid; they are generally attributed with performing the intracranial movements associated with kinetic skulls and with depressing the lower eyelid (Haas, '73). In *Trachydosaurus*, four deeply situated muscles comprise the group: 1) M. protractor pterygoidei, 2) M. levator pterygoidei, 3) M. levator bulbi dorsalis, and 4) M. levator bulbi ventralis. The M. levator bulbi dorsalis extends from the anterior end of the prootic to the lower eyelid; it will not be described further. The other three muscles insert onto the palate and pterygoid and will be considered in detail.

M. protractor pterygoidei (MPPT, Figs. 6, 8, 9)

The M. protractor pterygoidei is a small, but well-developed, triangular muscle. It originates partly from the lateral side of the inferior process of the prootic and mainly from the lateral side of the basipterygoid process. Insertion is along the dorsomedial trough of the quadrate process of the pterygoid, posterior to the basipterygoid joint. More dorsally arising fibers pass posteroventrally to the distal insertion area. The more ventrally arising fibers course more nearly horizontally to the proximal insertion area. The fibers measure approximately 7–8 mm. In *Tiliqua*, the MPPT takes a slightly different origin and the whole muscle is more vertically oriented than in *Trachydosaurus* (see Haas, '73).

M. levator pterygoidei (MLPT, Fig. 8)

The short, vertically oriented M. levator pterygoidei is located along the medial aspect of the epipterygoid. The origin is via a short tendon mainly from the dorsomedial end of the epipterygoid and partly from the anterolateral end of the prootic immediately deep to the epipterygoid. Muscle fibers run directly inferior and insert onto the anterior, dorsomedial aspect of the quadrate ramus of the pterygoid just inferior to the ventral epipterygoid joint. The muscle fibers in the MLPT measure approximately 11–12 mm.

M. levator bulbi ventralis (MLBV, Fig. 8)

The slender M. levator bulbi ventralis shares a common origin with the M. levator bulbi dorsalis on the anterolateral end of the inferior process of the prootic. The MLBV diverges from its mate and passes anteroventrally to insert onto the dorsal surface of the membrane of the pyriform recess, between the palatal rami of the pterygoids.

M. depressor mandibulae (MDM, Figs. 2–4, 8, 9)

The thin mandibular depressor complex lies posterior to the large adductor mass and deep to the M. constrictor colli. The mandibular depressor has an anterior and a posterior part, both of which attach to a stout, short tendon on the dorsum of the retroarticular process. The cross-section of the more anterior portion of the depressor is triangular, with the apex attaching to the dorsal side of the supratemporal process and the base lying parallel to the integument. The fibers of the anterior part extend posteroventrally from their origin at the separation of parietal and squamosal along the supratemporal process to their insertion at the tendon of the retroarticular process; they are longer than those of the posterior part. The fan-shaped posterior portion of the depressor slightly overlaps the posterior edge of the anterior portion. It originates on the dorsolateral surface of the M. spinalis capitis and narrows straight ventrally to the stout tendon of insertion.

M. intermandibularis (MIM, Fig. 2)

The M. intermandibularis is an extremely thin sheet of parallel muscle fibers that lies superficially and transversely across the ventral surface of the mandibulohyoid and pterygoid muscles; it is divisible into anterior and posterior parts. The anterior MIM arises from a median raphe just posterior to the anterior extent of the M. geniohyoideus and extends posteriorly to almost the angulus oris; it is continuous with the posterior MIM. The anterior MIM is a fasciculate sheet that passes laterally toward the mandibular ramus. However, the muscle fibers interdigitate with and attach to the underlying M. geniohyoideus and do not reach the mandible. The posterior MIM is continuous across the midline and forms a complete (nonfasciculate) sheet of muscle. This part does not intermingle with deeper musculature. It lies across the hyoid complex and the ventral surface of the M. pterygoideus, and attaches laterally into connective tissue and into the deep side of the integument. As a whole, the MIM is delicate and easily destroyed in superficial dissection. Over much of its extent, it may be comprised of only a single layer of fibers. In our dissections, we found the MIM to be more similar to the form illustrated by Camp ('23) than to that shown by Poglayen-Neuwall ('54; see Haas, '73, p. 361).

DISCUSSION
Cranial mechanics

The skull of *Trachydosaurus* appears to be a superficially inflexible unit. Analysis of dissected specimens and films of feeding in *Trachydosaurus* show little intracranial movement (Gans, personal observation). Frazzetta ('62) noted that *Tiliqua* possesses an amphikinetic skull (i.e., movable joints between supraoccipital and parietal, and also between frontals and parietal and/or nasals and frontals). In *Trachydosaurus*, the anterior cranial elements are tightly interdigitated and bonded tightly to the thick integumentary armor. There is little evidence of anterior (mesokinetic) joint mobility. However, whereas there is relatively little flexibility in the cranial roof per se, there is potential for movement between the cranial roof and the braincase at the parietal-supraoccipital synchondrosis. This represents the classic metakinetic joint of Frazzetta ('62) and appears to be the site of greatest intracranial mobility in *Trachydosaurus*.

The posterior palatal region of the skull has three clearly flexible links with other cranial units: 1) the prootic-epipterygoid-quadrate ramus of the pterygoid joints, 2) the basipterygoid process-quadrate ramus of the pterygoid joint, and 3) the quadrate ramus of the pterygoid-quadrate joint (Fig. 1). Both dorsal and ventral ends of the epipterygoid permit some sliding movement, so that this element appears to form a flexible brace between the pterygoid and the anterior braincase, as is typical of lizards (Frazzetta, '62). The basipterygoid process is linked to the pterygoid by a relatively loose synovial joint; consequently, the quadrate ramus of the pterygoid can spread laterally to the extent permitted by the relatively solid quadrate attachment, or can shift slightly dorsally. Movements of the quadrate itself are severely limited by its relatively solid dorsal attachments to the supratemporal and paraoccipital processes. Thus, although some quadratic displacement may be possible at the pterygoquadrate joint, it appears to facilitate minor bending in the pterygoid arch during a heavy bite rather than rotation of the quadrate (streptostyly) to permit differential jaw openings (*sensu* Rieppel, '78). The notion of flexibility along the posterior palatopterygoid arch is supported by the well-developed conditions of the Mm. protractor pterygoidei, levator pterygoidei, and levator bulbi ventralis (Fig. 8), which may contribute active bending forces to this region.

The quadratomandibular joint does not appear to permit a great deal of propalineal translation or mediolateral joint motion at gapes of less than 10°. The condyles fit into a rounded rather than onto a flattened fossa and are braced anteriorly by the prearticular process of the mandible. Additionally, the fit of the coronoid process into the coronoid recess of the posterior palate restricts anterior and mediolateral displacements of the lower jaw. However, at gapes of greater than 10°, the mandible might have progressively greater degrees of freedom for both propalineal sliding and mediolateral deviation as it becomes increasingly free of the above-noted mechanical stops.

Trachydosaurus possesses a relatively simple, peglike dentition limited to the jaw margins; however, larger teeth are located more posteriorly in the tooth row. Such a size arrangement is not uncommon among larger extant lizards; in *Trachydosaurus* it would seem to facilitate the handling and crushing of larger, harder food items, such as snails. Whereas it readily takes such prey, *Trachydosaurus* remains an opportunistic omnivore (Cogger, '75), and does not show the radical dental, quadrate, or palatal morphology associated with a more specialized, shell-crushing mode of feeding (Dalrymple, '79).

The relative motions between the cranial components and those of elements of the integumentary armor are of interest. Whereas the armor travels with the snout in the anterior regions, it is separated substantially from the posterior portions of cranium and mandible (witness the heavy layers of fat and connective tissue). Kinematic analysis suggests that the integument here must therefore bend more extensively when the jaws open; this is facilitated by the hinges between the overlapping bony plates in the nuchal and ventral postmandibular regions which form drastically different connections than the butt joints seen more anteriorly.

Aponeuroses

The patterning of the various cranial aponeuroses is important from a functional viewpoint as these sheets both delineate muscles and determine the lines of action of fiber groups within whole muscles. Their arrangement is significant, as it could affect the force vectors produced by the number of fibers acting at any time. Numerous authors have used one aponeurosis in particular, the so-called basal aponeurosis (Bodenaponeu-

rose), as a guide for naming and homologizing portions of the external adductor musculature and establishing phylogenetic relationships (see Haas, '73; Iordansky, '70; Poglayen-Neuwall, '54; Rieppel, '80, '81; Rieppel and Gronowski, '81).

In the years since the monograph of Lakjer ('26), the literature describing aponeurotic-muscular relationships has become noncomparable and mainly nonfunctional, particularly with regard to the basal aponeurosis-external adductor complex. The degree of development and the complexity of the basal aponeurosis and its extensions vary substantially among species, as does the nature of the upper temporal arcade (Gomes, '74; Haas, '73; Rieppel, '80, '81; Rieppel and Gronowski, '81). Thus, criteria important in identifying points of homology are often obscured, whereas those reflecting functional divisions (e.g., topographically similar groups of muscle fibers) are usually ignored. Consequently, there is no general agreement on the methods of subdivision or illustration (see illustrations in Haas, '73, pp. 359–361, contrasting conditions in a single species illustrated by different authors) of this muscle mass (see below). Iordansky ('70) noted this and provided a purely mechanical and highly complex nomenclature that has not been generally accepted (Table 2). More recently, Gorniak et al. ('82) characterized the jaw muscles of *Sphenodon* in terms of both traditional muscle groupings and functional subdivisions, a method with much utility.

In *Trachydosaurus*, the unique and complex form of the coronoid aponeurosis further complicates traditional nomenclature. This situation is particularly vexing, as this species shows a remarkable hypertrophy of its main adductor musculature, much of which cannot be divided unequivocally by the standards used in the literature (e.g., the M. adductor mandibulae externus, see below), whereas other terms commonly applied prove to have little utility (e.g., the M. levator anguli oris, see below). For these reasons, our descriptions have proceeded topographically, with the aim of identifying mechanical units (*sensu* Gans, '69), and these have then been named within the broad framework provided by the traditional literature. Thus, we view the M. adductor mandibulae externus of *Trachydosaurus* as being composed of four discrete parts, whereas the M. adductor mandibulae internus is composed of two muscles (the Mm. pseudotemporalis and pterygoi-

TABLE 2. *Synonymy of the divisions of the external adductor of* Trachydosaurus *and of those described for other lizards*

Trachydosaurus	Traditional subdivisions[1]	Mechanical subdivisions[2]
MAME-1		
Lateral portion	M. adductor mandibulae externus superficialis (part 1b of the external adductor)	IIC, IID, IVH, IVI
Medial portion	M. adductor mandibulae externus medialis (3a head)	IID, IIE
	M. adductor mandibulae posterior	IVI
MAME-2		
Slip to lateral rictal plate	M. levator anguli oris (part 1a of the external adductor)	M. levator anguli oris
Main muscle mass	M. adductor mandibulae externus medialis (part 2 of the external adductor)	IA, IB, IID, IIIF
MAME-3	M. adductor mandibulae externus profundus (3b head)	IIIF
MAME-4	M. adductor mandibulae externus profundus (3c head)[3]	IIIF, IIIG

[1]Based accounts in Haas ('73) and Rieppel ('80, '81).
[2]Based on Iordansky ('70).
[3]In certain genera, some fibers of the head 3c may insert onto the lateral surface of the basal aponeurosis (Rieppel, '80). This condition is unusual in lizards.

deus, each subdivided into two parts). The Mm. depressor mandibulae and intermandibularis each contain two parts, whereas the Mm. levator anguli oris and adductor mandibulae posterior do not exist as distinct entities. The following section will take up terminological questions and attempt to establish the homologies for the units implicitly recognized here.

Musculature

In the traditional descriptions of the jaw adductor muscles of lizards, the external adductor mass is normally subdivided into superficialis (part 1), medialis (part 2), and profundus (part 3) portions, based on 1) the areas of insertion of muscle fibers relative to a basal aponeurosis (Bodenaponeurose) and/or the lower jaw, and/or 2) the origins of the fibers relative to parts of the upper temporal arcade (Haas, '73). Generally, the muscle fibers inserting onto the medial side of the basal aponeurosis have been assigned to the profundus portion of the external adductor, those fibers attaching to the lateral side of the basal aponeurosis have been termed the medialis portion of the external adductor, and those inserting most laterally and superficially have been denoted the superficialis portion (Table 2).

The present description of the musculature of *Trachydosaurus* utilizes the various parts of the coronoid aponeurosis as major topographical landmarks in subdivision of the external adductor into mechanical units. Our part IV of the coronoid aponeurosis corresponds to "the" basal aponeurosis of others, generally defined as a large, vertical (parasagittal) tendon sheet that attaches to the coronoid process, extends posterodorsally (often approaching or entering the posttemporal fossa), and splits the external adductor mass into medial and lateral portions (Gomes, '74; Haas, '73; Rieppel, '80, '81; Rieppel and Gronowski, '81).

The superficialis portion of the external adductor is traditionally divided into two parts: 1) the M. levator anguli oris (M. retractor anguli oris; 1a portion of the external adductor), which attaches to the angle of the mouth and other superficial tissues, and 2) the superficialis part proper (1b portion of the external adductor), which attaches onto the lateral aspect of the lower jaw (Haas, '73). In *Trachydosaurus*, only a superficial, thin slip of the MAME-2 attaches onto the edge of the lateral rictal plate (rather than curving medially with the remainder of the muscle mass to insert onto part Ia of the coronoid aponeurosis) and thus corresponds to a M. levator anguli oris. Dorsally, this is contiguous with the rest of the MAME-2; we do not recognize it as a separate muscle, although it lies in the position in which a M. levator anguli oris has been described in the literature (Haas, '73; Poglayen-Neuwall, '54). The lateral part of the MAME-1 inserts in part onto the lateral side of the mandible and in part onto the

medial surface of part Iv of the coronoid apo-
neurosis; it is the muscle traditionally re-
ferred to as the M. adductor mandibulae
externus superficialis. However, this zone is
continuous with the deeper portion of the
MAME-1; their separation would again have
to be arbitrary.

The medialis portion of the external adduc-
tor is traditionally defined by its position
lateral to the basal aponeurosis (Haas, '73).
In *Trachydosaurus*, the MAME-2 lies lateral
to the basal aponeurosis (part IV of the coron-
oid aponeurosis) and thus is comparable to
the medialis portion of the external adductor.
Also, the deeper part of the MAME-1 (attach-
ing onto structures medial to the middorsal
line of the mandible) should be included in
the grouping traditionally named the M. ad-
ductor mandibulae externus medialis, head
3a. (In contrast, note the comments above
regarding the M. adductor mandibulae exter-
nus superficialis; also see below.)

The profundus portion of the external ad-
ductor tends to be divided into three heads
(3a, 3b, and 3c), each with a distinct area of
origin, but all inserting medial to the basal
aponeurosis (Lakjer, '26). The 3a head origi-
nates from the anteromedial quadrate and is
the most laterally situated part of the profun-
dus portion. Haas ('34) reevaluated Lakjer's
assignment of the 3a head and considered it
to be more appropriately a part of the medi-
alis portion. Rieppel ('80, '81) concurred with
Haas. In *Trachydosaurus*, part of the medial
portion of the MAME-1 may correspond to
the traditional 3a head; however (as noted
above), this is by no means a distinct or sep-
arate muscle belly. The 3b head originates
from the dorsal margin of the posttemporal
fossa and this is equivalent to our MAME-3.
However, the distal end of part IV of the
coronoid aponeurosis (the basal aponeurosis)
extends well into the posttemporal fossa and
here rotates medially so that the MAME-3
inserts onto the dorsal side of the basal apo-
neurosis rather than onto its "traditional"
medial aspect. Its distinctive origin suggests
that the MAME-3 is likely to be the equiva-
lent of the 3b head of the profundus rather
than a portion of the medialis. The 3c head
of the profundus portion is defined as origi-
nating from the prootic and the paraoccipital
process. The MAME-4 of *Trachydosaurus*
arises from these areas, inserts entirely on
the medial and ventromedial portions of part
IV of the coronoid aponeurosis, and appears
to be directly comparable to the traditional
3c head.

The internal adductor mass of *Trachydo-
saurus* is divided into the Mm. pseudotem-
poralis and pterygoideus, based on the
positions of these muscles medial to the max-
illary and mandibular divisions of the tri-
geminal nerve, and on their general topog-
raphy. These muscles are straightforward
equivalents to the muscles traditionally so-
named in other lizards.

The M. adductor mandibulae posterior is
the smallest of the three major traditional
portions of the adductor complex. In many
lizards, this muscle lies posterolateral to the
mandibular division of the trigeminal nerve;
however, it is not always found or definable
(Haas, '73). *Trachydosaurus* lacks a posterior
adductor. However, the prootic belly of the
MAME-1 may be the equivalent of the pos-
terior adductor of other lizards. This muscle
area is partly separated from the rest of the
MAME-1 by part III of the coronoid aponeu-
rosis, and it lies posterolateral to the mandi-
bular nerve, in the "traditional position."
However, as this belly is continuous with the
rest of the MAME-1, and its fibers have
equivalent angles and fiber length, there is
no real reason for separating it and recogniz-
ing it as a distinct muscle.

Utility

Separation of the muscles of mastication
into distinct subcategories can serve various
usages. Breakdown for taxonomic purposes,
as provided in the traditional system of Camp
('23), and functional separation (see Gorniak
et al., '82) are obvious variants. What is most
important is the determination of homogene-
ity of structure and the assumption that this
may be reflected in homogeneity of action.
With the discovery of discrete, although mor-
phologically not obvious fiber types (and mo-
tor units), the pattern is no longer discernible
by inspection (Gans, '82). However, although
differences may be masked, their discovery,
perhaps in terms of fiber units arranged at
distinct angles and with distinct fiber
lengths, provides an obvious clue that activ-
ity may differ (cf. Gorniak et al., '82). The
traditional method of subdividing the adduc-
tor musculature (into components useful for
establishing homologies) is inadequate for
such an analysis in *Trachydosaurus*, because
it relies on the position of the muscles rela-
tive to other structures (e.g., divisions of the
trigeminal nerve, parts of the cranial roof)
rather than on the morphology of the mus-
cles themselves. In contrast, the topographi-
cal pattern disclosed by the present kind of
morphological analysis should allow some
level of functional prediction.

The present data suggest that the muscu-
lature of *Trachydosaurus* shows relatively

slight medial to lateral differentiation in fiber lengths. Rather, the lengths of fiber groupings change gradually on anteroposterior axis correlated in some way with fiber curvature. None of the muscles show the remarkable heterogeneity recently characterized for the M. pterygoideus of *Sphenodon* (Gorniak et al., '82). This suggests that the complexly pinnate adductor musculature of *Trachydosaurus* represents primarily an enhancement of the strength of the bite, rather than a complication of the movement pattern. This correlates with the relatively simple motion observed in behavioral studies (Gans, personal observations). What is most important in the present system is that the entire adductor musculature would appear to represent a single set of graded mechanical units so that one would expect contraction waves to proceed posterodorsally as the muscles are being recruited during the bite. Therefore, one should be able to observe a matching of the muscular length-tension relations to the fiber-length relationships of the muscle masses.

Whereas some relatively small residual portions may reflect homology (for instance, "the M. levator anguli oris" may well be the remnant of a once more distinct muscle), the present kind of study cannot document this with any certainty. Mapping of such muscular remnants will, in the future, require utilization of HRP (horseradish peroxidase) techniques, in the expectation that the cell bodies of the motoneurons of discrete muscles will generally occupy discrete (though possibly overlapping) central motor nuclei.

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