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The Functional Anatomy of a Permian Dicynodont

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THE FUNCTIONAL ANATOMY OF A PERMIAN DICYNODONT

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A specimen of *Dicynodon trigonocephalus* from the Madumabisa mudstones of Zambia is described.

The jaw adductor musculature is reconstructed. It is concluded that two slips of the adductor externus medialis were present. A posterior adductor ran from the quadrate to the medial surface of the lower jaw and a forwardly running muscle may have inserted on the reflected lamina of the angular. The masticatory cycle is much as Crompton & Hotton (1967) proposed, but new interpretations are developed for the movable quadrate and the W-shaped jaw hinge. It is proposed that the horny jaw covering inserted into the longitudinal dentary sulcus.

The reflected lamina of the angular is discussed. As well as being a possible site for adductor muscle insertion, it is also suggested that hyoid musculature attached to it.

The nasal capsule and cranial nerves and blood vessels are described.

The forelimb and pectoral girdle are described and the main muscles reconstructed. It is concluded that the principle movements of the forelimb were protraction and retraction with only a small degree of long axis rotation. Rotation of the glenoid to lengthen the stride may have occurred. Flexion and extension of the lower limb was a particularly powerful action, but in contrast protraction and retraction were not powerful. The pectoral girdle and forelimb are seen as providing a stable and strong base for the massive anterior part of the body, but not generating much locomotory thrust.

In contrast the hindlimb is supplied with musculature (the ilio-femoralis) that generates a powerful locomotory thrust by retraction and long axis rotation. The caudi-femoralis is much reduced but the ischio-trochantericus muscle has assumed importance in pulling the femur postero-ventrally. The pubo-ischio-femoralis externus is in a less advantageous position to do this and has assumed a role largely of a ventral adductor.

In the axial skeleton, rotation of the head may occur, to a limited extent, between the atlas neural arch and the odontoid. The neck is a flexible region but the neck vertebrae bear strong transverse processes for origin of the extensive musculature that supports the head. However, the trend more posteriorly is to limit flexibility of the vertebral column by more vertically oriented zygapophyses and by ligamentous and muscular ties between vertebrae. The insertions of the longissimus dorsi have been modified from the presumed primitive condition and occupy only the dorsal surface of the transverse process.

There are five sacral vertebrae. The centra of the first four are fused. The fifth is free. The anterior and posterior zygapophyses are reduced. The neural spines become longer antero-posteriorly, but very narrow transversely. The sacral ribs are all expanded but not fused either to the ilium or to the centra.

The caudal region consists of possibly thirteen vertebrae and is probably complete. Ribs are present up to the fifth caudal vertebra. From vertebra 6 backwards haemal arch facets are seen on the centra.

It is concluded that *Dicynodon trigonocephalus* was a slow-moving herbivore, nevertheless capable of a sustained locomotory effort. It may have avoided predators by crepuscular or cryptic behaviour. The powerful masticatory mechanism of *D. trigonocephalus* would have allowed exploitation of tough and bulky food sources.

The relationships of *D. trigonocephalus* are discussed. It is possible that it is a close relative of the Permian stock that gave rise to *Lystrosaurus*.

INTRODUCTION

The dicynodonts were a group of herbivorous mammal-like reptiles, successful in Permian and Triassic times. Their distribution was wide though species diversity diminished dramatically at the Permo-Triassic boundary. In size they ranged from, for example, *Diictodon sesoma* (Watson 1960) with a reconstructed vertebral column length of 45.0 cm, to *Stahleckeria potens* (von Huene 1944) with a length of 360.0 cm. Although extinct they are well represented in the fossil record in number and diversity.

The dicynodonts are particularly interesting in that they constitute the first successful major radiation of terrestrial animals into herbivorous niches. They are therefore a potentially valuable group for investigating the processes and mechanisms of evolution as illustrated by the fossil record. In recent years numerous hypotheses, with varying degrees of evidence, have been put forward in an attempt to explain various aspects of how phylogenesis is brought about by evolution. There are, for example, the theories of punctuated equilibria (Eldredge & Gould 1972), adaptive experimentation (Schaeffer 1965), adaptive zones and key innovations (Bock 1965), and undirected selection (Raup & Gould 1974). Also much discussion concerning the evolutionary species concept, recently reviewed by Wiley (1978), has taken place. A sufficiently well known group of fossils, like dicynodonts, should shed considerable light on these theories and generate yet others concerning, for instance, the nature of a group that gives rise to an adaptive radiation, or the tolerance of diversity within a habitat.

However, until recently, understanding and detailed knowledge of dicynodonts has been slow to progress, particularly in the two areas of taxonomy and functional anatomy.

Various advances in the taxonomy of dicynodonts have been made recently. Work by Keyser (1975) has reorganized the genus *Oudenodon* and other tuskless genera; Cluver & Hotton (1980) have started to elucidate the relations of the major Permian dicynodont genera *Oudenodon, Dicynodon, Diictodon* and *Kingoria*; Keyser & Cruickshank (1979) have reorganized the Triassic dicynodont families; and work in progress by M. A. Cluver and G. M. King attempts to determine the relationships of the *Tapinocephalus* zone forms.

A pattern of the overall relationships and evolution of dicynodonts is therefore emerging.

Unfortunately, even though natural groups and well defined genera are becoming apparent, little work has been carried out that attempts to determine which particular available niche a particular dicynodont form occupied. This is partly due to the scanty nature of the detailed information available about the Permian and Triassic palaeoenvironment. Probably more to blame is the lack of rigorous functional–morphological studies of dicynodont osteology. There have been exceptions to this, for example, Crompton & Hotton (1967), Cox (1972) and Cluver (1978), yet a detailed study of the postcranial skeleton of a generalized Permian dicynodont is still lacking. The present paper sets out to correct this by a functional study of one well preserved Permian dicynodont, *Dicynodon trigonocephalus*. An ecological interpretation of the results of this study is also given.

DICYNODON TRIGONOCEPHALUS: IDENTIFICATION AND PRESERVATION

The specimen to be described, TSK 14, was collected from field locality 1 in the Madumabisa mudstones of the Karoo deposits of the Luangwa Valley, Zambia (Kemp 1975).

It is thought that the localities where dicynodonts were collected correspond to *Daptocephalus* zone (Kitching 1977) localities of the South African Karoo deposits, mainly because a specimen of *Procynosuchus delaharpeae* (Kemp 1979) was found in association with the dicynodonts. However, Keyser & Smith (1978) have recommended reorganization of the Karoo into a series of biozones, and they report *Procynosuchus* from deposits below Kitching's *Daptocephalus* zone, in the biozone that they call the *Aulacephalodon* assemblage zone. The dicynodonts in Kemp's collection may therefore represent upper *Cistecephalus* zone or lower *Daptocephalus* zone (both *sensu* Kitching (1977)) or possibly both.

TSK 14 is the almost complete skull and lower jaw and most of the postcranial skeleton of a medium-sized dicynodont. It has suffered some weathering. The vertebral column is complete from the atlas to the presumed tip of the tail. The dorsal and sacral vertebrae are in extremely good condition. The anterior ten vertebrae are damaged to varying degrees. Almost all rib-heads are present, a few bearing shafts of considerable length. All elements of the pectoral girdle are present, including a well preserved clavicle, both scapulae, coracoids and precoracoids. Humerus, radius and ulna are present in good condition, together with some elements of the manus. Both sides of the pelvis, together with both femora, are preserved, the left ilium being in particularly good condition. No tibia, fibula or pes is present. TSK 14 conforms to Cluver's (1977) definition of the genus *Dicynodon* in the following ways: the lower jaw has a dentary sulcus and probably dentary tables (the specimen is broken in this region); the palatal rim is unnotched; tusks are present; the large palatines meet the premaxilla; the interpterygoid vacuity is short; the intertemporal region is constricted. The condition of the septomaxilla in TSK 14 does not conform to that of *Dicynodon*, however, since it is recessed within the nostril, although not deeply.

Since no specific revision of *Dicynodon* has been attempted, further diagnosis rests on comparing TSK 14 with other described specimens. The unusual features of TSK 14 were assessed to be:

(1) the skull is broader than it is long;
(2) the temporal fenestra is shortened;
(3) the parietals are not exposed on the skull roof;
(4) the snout is robust and rounded.

When the described type specimens are examined it is apparent that the type of *D. trigonocephalus* agrees well with TSK 14 in overall shape and size and by having a short temporal fenestra, by the postorbitals overlapping the parietals, and by the snout being robust and rounded. The type of *D. trigonocephalus* in the Rubidge Collection (R.C. 38) also displays further similarities with TSK 14:

(1) the relative interorbital and intertemporal widths;
(2) prefrontal bosses;
(3) no frontal bosses;
(4) the postorbital bar is turned slightly backwards;
(5) the palatine is of a similar shape;
(6) a labial fossa is present;
(7) the quadrate ramus of the pterygoid is very deep;
(8) the basioccipital tubera have squared-off ends;
(9) the basicranial axis is shortened.

TSK is therefore extremely similar to *D. trigonocephalus* and is assigned to this genus and species pending revision of the genus.

TSK 14 has several other unusual features, which may be present in R.C. 38 but at this time cannot be seen as the specimen is not completely prepared. These features are:

(1) shortening of the interpterygoid vacuity;
(2) a ridge running between the basioccipital tubera;
(3) an extremely deep lower jaw symphysis;
(4) a lateral dentary shelf that almost occludes the intramandibular fenestra;
(5) a forwardly directed retroarticular process.

Also the tusk is more downwardly pointing in R.C. 38 than in TSK 14, but this may be due to distortion in the latter, or it may represent a distinguishing character of the Zambian specimen.

Until the genus *Dicynodon* is revised, TSK 14 may therefore be considered to be a specimen of *Dicynodon trigonocephalus*, with the following diagnosis:

infraorder	Dicynodontia
family	Dicynodontidae
genus	*Dicynodon*
species	*trigonocephalus* (Broom 1940)

Medium to large skull, width greater than length; postorbitals overlap parietals completely on the skull roof; prefrontal bosses present; labial fossa present; shortened basicranial axis; deep quadrate ramus of the pterygoid; ridge running between basioccipital tubera; lower jaw with extremely deep symphysis and a lateral dentary shelf almost occluding the Meckelian fossa; forwardly directed retroarticular process. Horizon: probably *Daptocephalus* zone (*sensu* Kitching 1977).

The entire specimen was prepared in acetic acid (Toombs 1948; Rixon 1948) and strengthened with a 10% solution (by volume) of polybutylmethylacrylate in ethylmethyl ketone.

The specimen is housed in the private collection of Dr T. S. Kemp in the University Museum, Oxford.

FUNCTIONAL ANATOMY

The skull

(i) *Description*

Although a comparative study of the dicynodont skull has not been attempted here, certain specimens have been used for comparison to highlight the unusual features of *Dicynodon trigonocephalus*, or to provide information about structures that the specimen of *D. trigonocephalus* lacks. The other dicynodont specimens referred to belong to Dr T. S. Kemp's collection and have been prepared mechanically by the author. They are TSK 67 and TSK 104, identified as *Oudenodon bainii* (*sensu* Keyser 1969), both being exceptionally well preserved skulls and lower jaws (King 1979).

Parts of the skull of *D. trigonocephalus* are poorly preserved and some sutures are indistinct. However, very little of the skull is missing completely (figures 1–13).

The skull is unusual in being wider than it is long. These proportions are produced both by broadening of the back of the skull and by reduction along the longitudinal axis of the skull. The squamosal is of the typical dicynodont pattern except that the zygomatic branch of the squamosal is short and, together with the broadening of the back of the skull, this produces an extremely short but wide temporal fenestra. As the postorbital bar has a slight backward tilt, produced by a marked twist along its length, this also decreases the length of the fenestra (figure 2).

The orbits are large, oval and face antero-laterally. There is a marked prefrontal boss extending into the orbit above the lachrymal foramen. Its lateral surface is covered with deeply pitted, roughened bone.

Just behind the level of the postorbital bar on the skull roof is the small pineal foramen (figure 1: pin.). Anterior to this is the squarish preparietal, marked by a central depression. The depression is bordered at either side by low ridges formed by the preparietal together with the parietal posteriorly and the frontal anteriorly. Anteriorly there is also a small boss formed at the junction of preparietal and frontals.

The postorbitals overlapping the parietals completely on the skull roof is another distinguishing feature of *D. trigonocephalus*. Dorsally, the posterior edge of the postorbital sweeps inwards and backwards as a sharp, almost vertical, ridge to cover the parietal of its side completely, and to meet the postorbital of the opposite side. The postorbital is prevented from reaching the squamosal by the parietal. The intertemporal bar so formed is relatively narrow compared with the interorbital width and with the intertemporal regions of other dicynodonts. It is, however, almost unique in being composed superficially solely of the postorbitals. Either side of the midline the postorbitals slope away ventro-laterally at an angle of approximately 30° to the horizontal. The intertemporal bar is therefore approaching the condition seen in *Kannemeyeria* (Pearson 1924) although obviously not so marked.

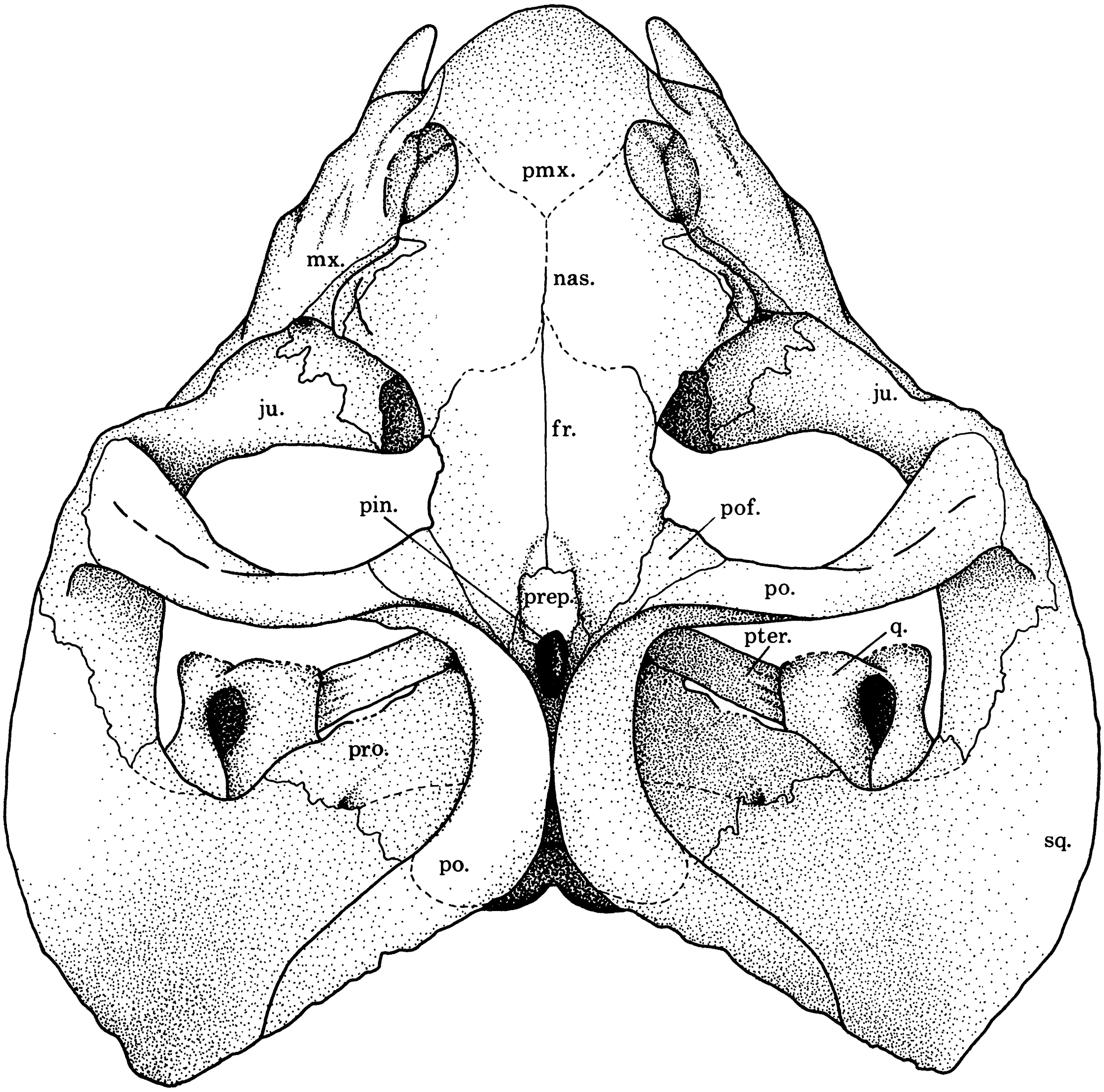


FIGURE 1. Dorsal view of the skull. (Two-thirds natural size.)

The palate (figure 3) is remarkable in that it shows very well the shortening of the skull behind the interpterygoid vacuity. Comparison with the *Oudenodon* specimens indicates that the skull anterior to this point is not shortened at all.

The palatal surface anterior to the choanae bears a median premaxillary ridge which reaches its highest point where the premaxilla meets the thin median plate of the vomer. The anterior maxillary, premaxillary and palatine ventral surfaces are marked with numerous fine pits and striations, presumably correlated with a horny palatal covering. The bulbous anterior part of the palatine (figure 3: bu. pal.) is separated from the anterior ramus of the pterygoid and from the ectopterygoid by a spur of the maxilla (figure 3: mx. sp.).

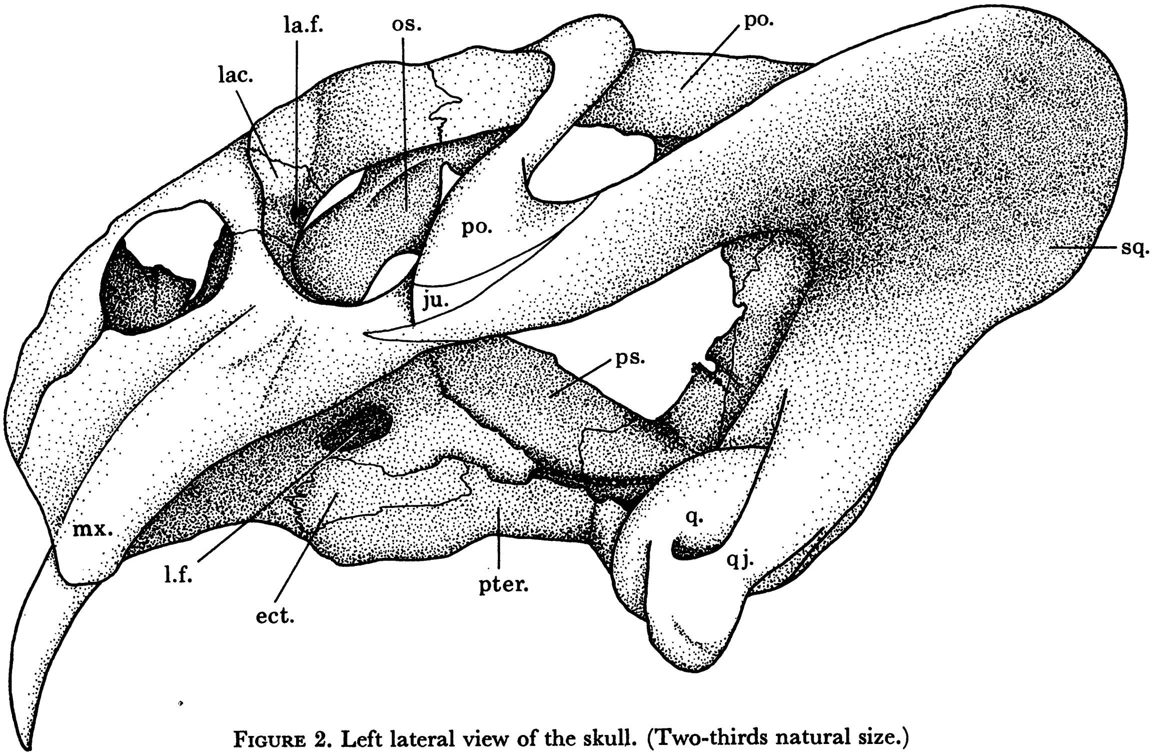


Figure 2. Left lateral view of the skull. (Two-thirds natural size.)

D. trigonocephalus is unusual in having a labial fossa (figure 3: l.f.) similar to that of *Lystrosaurus* described by Cluver (1971). The fossa is contained mainly within the palatine, the jugal (a very extensive bone here compared with *Lystrosaurus*) forming the antero-lateral border. The fossa is oval and opens into the maxillary–jugal cavity (see page 34).

The quadrate rami of the pterygoids are worthy of attention in that they are particularly short, barely reaching the quadrate, and leave the body of the pterygoid at an angle of approximately 120°, compared with 150° for *Oudenodon*. The pterygo-paroccipital foramen (figure 3: p.p.f.) is almost occluded since the extremely deep quadrate ramus (it is more plate-like than rod-like, in contrast to that of most dicynodonts) and the epipterygoid attached dorsally to the pterygoid closely approach the prootic.

The basisphenoid–basioccipital tubera project ventrolaterally.

The basicranial axis (figures 2, 4) shows the normal dicynodont features of *Oudenodon*. However, it is relatively short, especially in the region posterior to the quadrate ramus of the pterygoid, and the parasphenoid rostrum rises higher in the skull. The dorsal processes of the vomers, which clasp the anterior extremity of the parasphenoid, also turn dorsally very abruptly and extend above the parasphenoid for almost 1 cm and contact the orbitosphenoid. In *Oudenodon* a wide gap, presumably filled with cartilage in life, exists between vomer and orbitosphenoid.

The back of the skull is very wide relative to that of *Oudenodon*, and this broadening seems to stem not from a thickening in the latero-medial extent of any of the bones (prootic, parietal, squamosal) that form the sidewall of the braincase and anterior occipital surface, but rather from a reorientation of these bones, as they lie almost at right angles to the line of the basicranial axis, instead of about at 40° to it as in *Oudenodon*. This might be expected since the observed shortening of the basicranial axis posterior to the interpterygoid vacuity would cause a great reduction in length of the braincase and necessitate some compensatory increase in width.

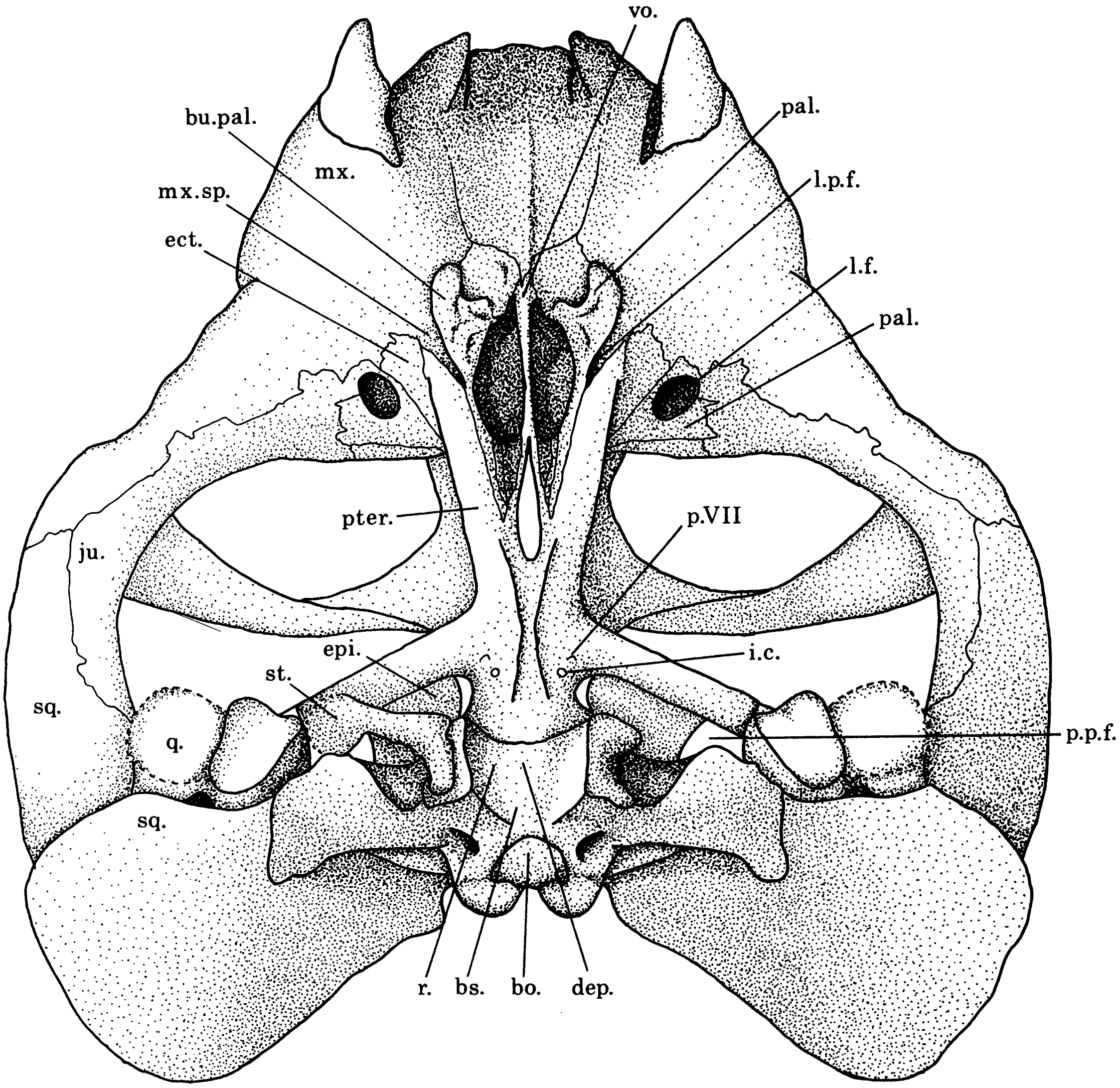


Figure 3. Palatal view of the skull. (Two-thirds natural size.)

Both stapes (figure 5) are damaged, but the left the less so. It is approximately a rectangular block, with a semicircular excavation in the dorsal half. The distal end is oval in outline and continuous with a triangular facet on the distal half of the posterior face. The proximal end (figure 5*e*) is a flattened, oval facet, orientated parallel to the transverse plane of the bone, but posteriorly extending up into a dorsal process (figure 5*a*: d.p.). The bone surface is badly damaged and shows little detail, but there is a pronounced channel on the dorsal process (figure 5*a*, *f*:ch.). No stapedial foramen is present.

The canine tusk measures 39 mm below the surrounding collar of maxilla. The tusk extends at least 36 mm above this, into the maxillary jugal cavity. In cross-section it is oval and shows concentric layers of dentine varying in thickness from one to several millimetres. There is a central oval pulp cavity. No enamel is present. The tusks both show extensive wear facets on their medial sides. The facets occupy at least half the length of the exposed tusk and take the form of a completely flat surface, as if caused by abrasion in a parasagittal plane. The tusks are gently curved and face forwards as much as downwards. The line of the tusk is continued postero-dorsally in the maxilla as a stout, rounded ridge.

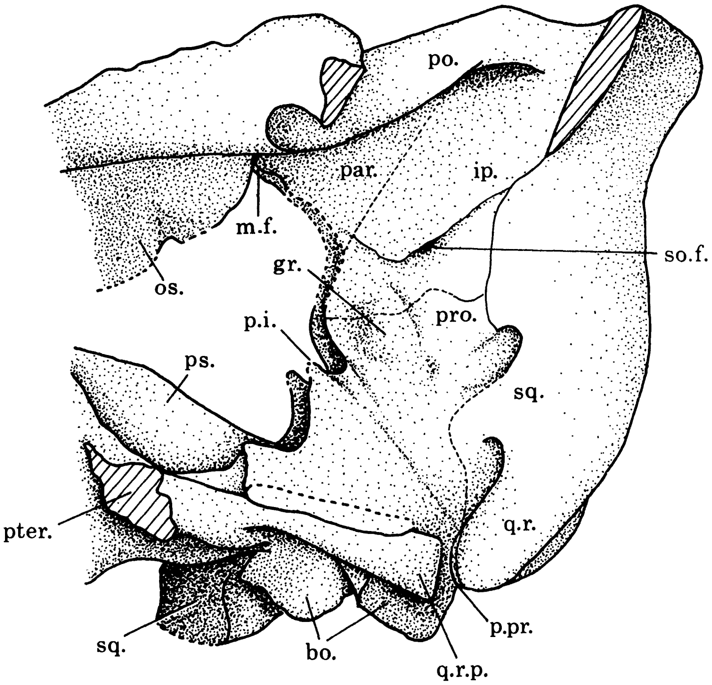


FIGURE 4. A partial reconstruction of the braincase seen in left postero-lateral view. The zygoma and postorbital bar have been removed. (Two-thirds natural size.)

The lower jaw (figures 6–9) is massively built, with a strong symphysis. The height of the jaw ramus decreases towards the jaw hinge, giving this a rather weak appearance.

As there is a transverse break through the symphysis, four foramina have been revealed on the broken anterior face. Two smaller circular foramina are found on the midline, one approximately halfway between dorsal and ventral edges of the symphysis, and the other nearer the dorsal edge and flanked by the remaining two, dorso-ventrally elongate foramina (figure 9: c.1, c.2). The latter open internally on each jaw ramus as large gaps between the V-shaped splenial and the prearticular (figure 9: g.), and are probably connected with the housing of Meckel's cartilage. The upper circular foramen opens internally as a gap on the midline between dentary and splenial (figure 9: d.g.). The internal opening of the lower circular foramen cannot be seen but it is probably in the splenial at the bottom of the deep, median splenial recess (figure 9: s.r.).

(ii) *The jaw musculature*

Several authors have attempted to reconstruct the jaw muscles of dicynodonts (Crompton & Hotton 1967; Cluver 1971, 1975; Barghusen 1976). Generally it is agreed that it is possible to reconstruct the external adductor in two slips, medial and lateral, and of the internal adductor the anterior and posterior pterygoideus muscles are usually indicated. In the following account the terminology of Crompton & Hotton (1967) will be used.

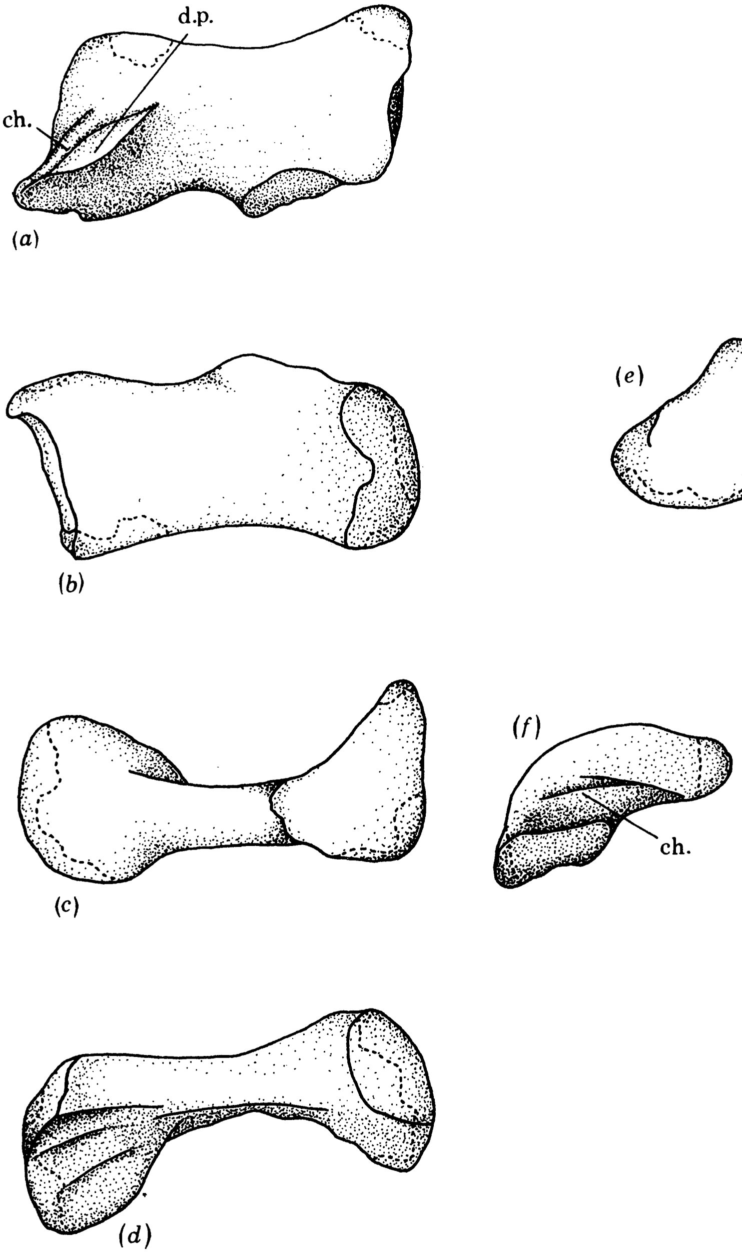


Figure 5. The left stapes (magn. × 2): (*a*) dorsal; (*b*) ventral; (*c*) anterior; (*d*) posterior; (*e*) proximal; (*f*) distal.

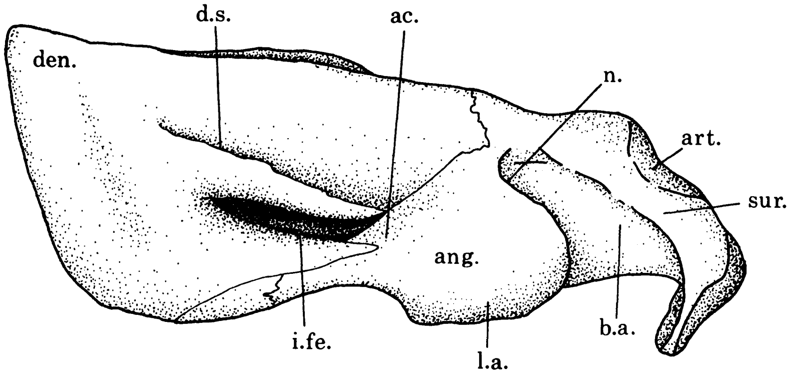


FIGURE 6. Lower jaw in left lateral view. (Two-thirds natural size.)

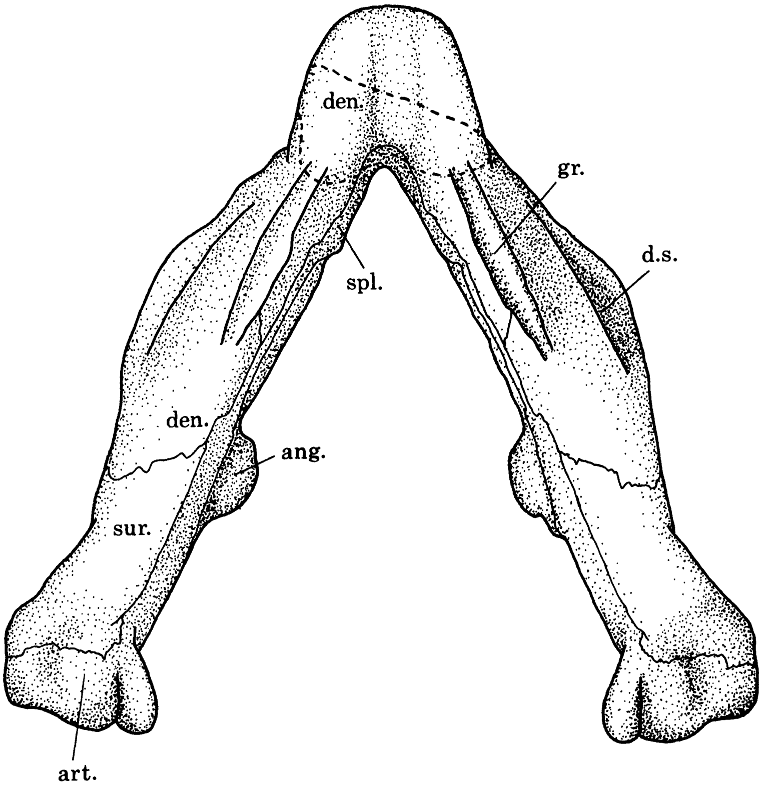


FIGURE 7. Lower jaw in dorsal view. The broken line represents the broken edge of the specimen. (Two-thirds natural size.)

Normally the sites of insertion and origin of muscles have been determined by comparison with extant reptiles or mammals, and by attempting to identify muscle scars on the bone. Microscopical examination of the dicynodont specimens available (*D. trigonocephalus* and the two *Oudenodon* specimens) indicate that several kinds of bone marking occur.

(1) The bone surface is smooth and shiny, unmarked or bearing only fine, regular striations. This is found on parts of the skull roof and braincase, and probably indicates bone with no special attachments.

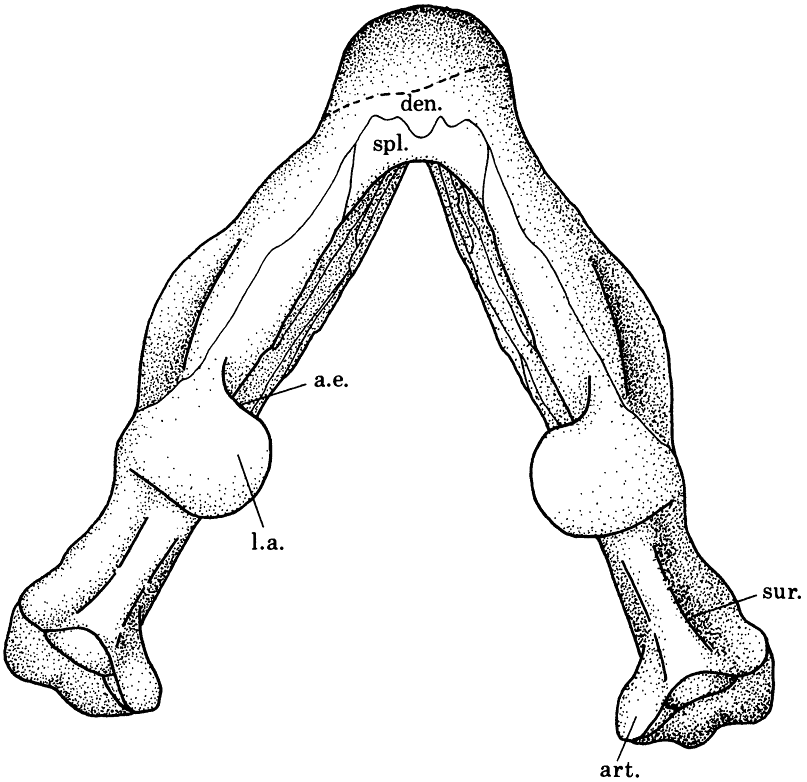


FIGURE 8. Lower jaw in ventral view. Broken line represents the broken edge of the specimen. (Two-thirds natural size.)

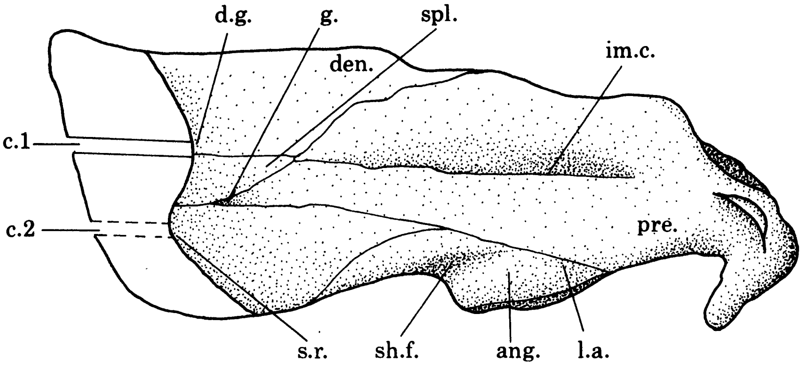


FIGURE 9. Lower jaw, medial view of the right side. The unshaded portion represents the symphysis. (Two-thirds natural size.)

(2) The bone is covered by masses of very small foramina, and is often itself corrugated. This surface is found on the snout and is probably connected with covering of the bone by horn or closely applied scales.

(3) The bone surface is generally smooth but porous because of the presence of many small foramina. In the *Oudenodon* specimens a pink coloration was often associated with this type of surface. It is found on the occipital and jaw condyles, and other parts of the occiput and braincase. It probably indicates a cartilage covering or continuation.

(4) The bone is marked by short, often deep, striations which are irregular in orientation and size, often forming whorls. Some small foramina may be present. The bone is not marked at such a high density as in the second category described, but the markings tend to occur in discrete patches, often merging into a bone texture like that described in the first category.

This fourth category bears most resemblance to the muscle scars found in modern reptiles and mammals. Such markings are indeed found on the dicynodont skulls in areas implicated as muscle attachment sites by other authors, for example, the squamosal of the posterior surface of the temporal fenestra, the anteriorly facing surface of the quadratojugal, the lateral surface of the pterygoid and ectopterygoid, the ventral depression on the pterygoid either side of the median pterygoid ridge on the palate, the occipital exposure of the squamosal above the quadratojugal. However, additional sites also show up, for example: the anteriorly facing surface of the quadrate; the ventro-lateral surface of the maxilla, extending onto the suborbital bar; the ventral surface of the basioccipital, between the tubera; the medial surface of the articular–prearticular below the median condyle; the lateral surface of the angular below the intramandibular fossa.

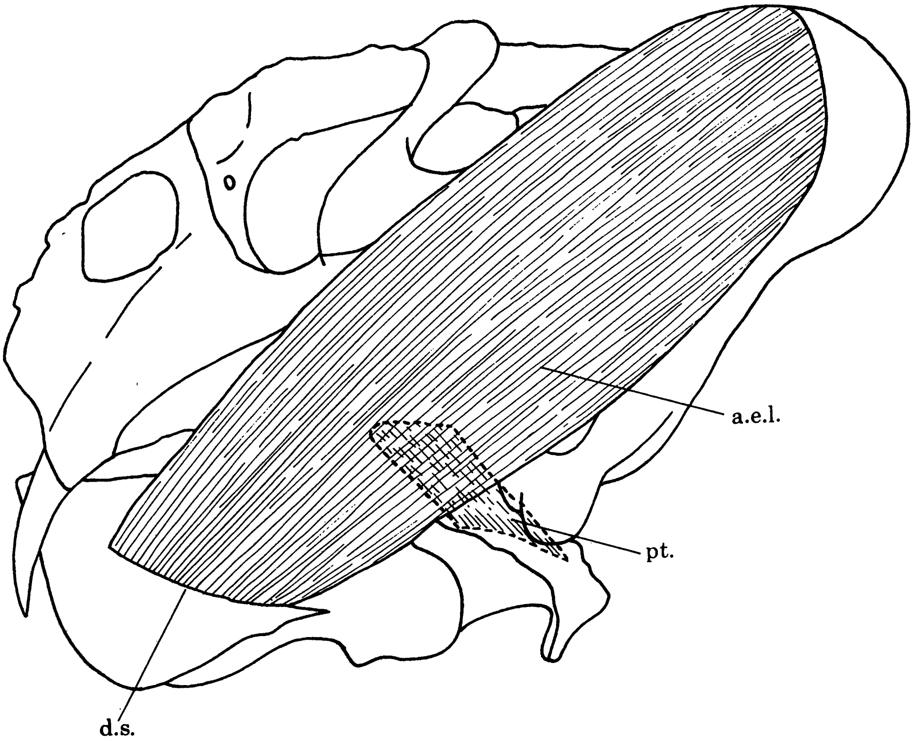


Figure 10. Diagram of some of the principal jaw muscles. (Half natural size.)

There are also two sets of markings that occur uniquely. These are the close, regular, fine striations found on the lateral surface of the reflected lamina of the angular, and the heavy, rugose striations seen on the lateral surface of the dentary just in front of the intramandibular fossa. This last feature is seen clearly in *Oudenodon*; in *D. trigonocephalus* this area of the lower jaw is built up into the lateral dentary shelf.

The categories of bone markings are far from being unambiguous but they should provide some indication as to where muscles do or do not attach. The following muscle pattern in *D. trigonocephalus* is therefore suggested.

The origin of the adductor externus lateralis (a.e.l.) is reconstructed as being the antero-lateral surface of the zygoma posterior to the postorbital bar (figure 10: a.e.l). The origin extends onto the antero-laterally facing sheet of the squamosal above the quadrate.

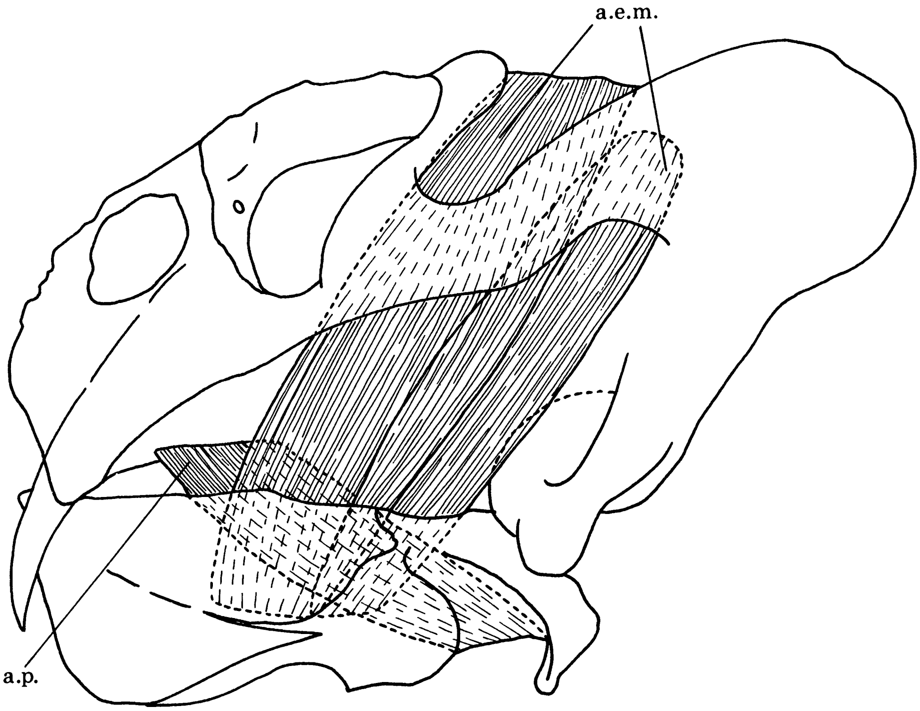


Figure 11. Diagram of some of the principal jaw muscles. (Half natural size.)

The insertion of the a.e.l. is taken to be the hollowed-out dorso-lateral surface of the lateral dentary shelf (figures 6, 7, 10: d.s.).

As reconstructed the a.e.l. is an extensive and powerful muscle which has an upward, backward and decidedly lateral pull.

The origin of the adductor externus medialis (a.e.m.) poses more problems (figure 11: a.e.m.). Usually its origin is reconstructed along the medial wall of the temporal fenestra, on the outer surface of the postorbital. In *D. trigonocephalus* the postorbitals meet in a crest in the midline, as described, and the apex of this crest bears fine, irregular striations, possibly indicating muscle attachment. This would seem likely as the postorbital crest is approaching the condition of the sagittal crest in mammals, which is a muscle-bearing structure. However, in addition, in *D. trigonocephalus*, there is a prominent oval recess beneath the postorbital where this meets the posterior wall of the temporal fenestra. Again this is marked by short, deep, irregular striations. It is possible therefore that a deeper slip of the a.e.m. originated from the oval trough, whereas the bulk of the musculature originated along the postorbital crest.

Cluver (1975) notes a similar origin site in *Chelydontops* but follows Barghusen (1973) in relating it to the pseudotemporalis muscle. In modern chelonians this muscle originates from the lateral surface of the epipterygoid. In *Sphenodon* and lizards a superficial component also originates from the anterior part of the superior temporal fenestra. However, in *D. trigono-*

cephalus the oval recess beneath the postorbital is posterior to the epipterygoid and in the posterior part of the temporal fenestra. It is therefore not an obvious homologue of the pseudotemporalis, and is here regarded as a slip of the a.e.m. *D. trigonocephalus* provides no evidence for the site of origin of the pseudotemporalis as the epipterygoid is badly damaged. In one of the *Oudenodon* specimens (TSK 67), however, the well preserved epipterygoid shows marking over the ventral half of the ascending ramus of the bone, possibly indicating the pseudotemporalis origin. If so, the origin is reduced compared to the probable condition in *Dimetrodon* (Barghusen 1973). The insertion of the pseudotemporalis is unclear. In *Dimetrodon* Barghusen reconstructs it in the adductor fossa on the medial jaw surface. In the dicynodonts there is no obvious adductor fossa, and the other suggestions by Barghusen, that the pseudotemporalis tendon joined the tendon of the anterior pterygoideus, may be more applicable. To return to the a.e.m., it is more difficult to elucidate the insertion of this muscle than the origin. In *Dimetrodon* the insertion is probably into a bodenaponeurosis attached to the coronoid eminence of the lower jaw. In dicynodonts various insertions have been postulated, including the longitudinal dorsal dentary groove (figure 7: gr.). For various reasons this is discounted as an insertion in the present specimen. The groove in *Dicynodon trigonocephalus* is rather narrow and high-walled. A fleshy insertion of the a.e.m. would therefore be very restricted in this groove, whereas the additional insertional area offered by the groove in contrast to a flat surface would not be particularly advantageous to a tendinous insertion. An alternative use of the groove in connection with the attachment of the horn covering of the lower jaw has been suggested previously, because of the similarity in structure of the lower jaw to that of chelonians. However, the horn covering the lower jaw of a turtle, *Chelonia mydas*, seems to be associated more with free-standing ridges, rather than a definite groove as in dicynodonts. However, this difference may reflect the different ways in which the horn covering is structured in chelonians and dicynodonts: in the former it is mostly a chopping ridge, in the latter it will be argued that the horn was also a shearing and grinding platform.

The inner surfaces of the walls forming the groove in dicynodonts are rather smooth, bearing fine striations, whereas the floor of the groove is pitted with irregular striations and pores. Anteriorly the groove levels out into the dentary table, and this bone surface is also deeply marked, as is the medial surface of the dentary at this point. The type of marking, high density foramina and striations is consistent with a covering of horn in this area.

It has been postulated elsewhere (King 1979) that the longitudinal dentary groove might have been the insertion of a bodenaponeurosis to which the a.e.m. attached. This is now discounted since the above morphological evidence is more in favour of a horn covering in the groove and also because an alternative site for the insertion of the a.e.m. is available.

If the dorsal and lateral surfaces of the dentary are ruled out as insertional sites for the a.e.m., the areas still available are the dorsal surface of the surangular, and the medial surfaces of the surangular and dentary.

In all other therapsids, and in *Dimetrodon*, the dentary is drawn up into a coronoid eminence or process associated with the insertion of the external adductors, often via a postulated bodenaponeurosis. But in only one early dicynodont, *Chelydontops* (Cluver 1975), is a coronoid process known. Cluver reconstructs the a.e.m. inserting on the coronoid process, but this helps little to indicate the position of the muscle in *Oudenodon* or *Dicynodon* since *Chelydontops* probably diverged from the ancestor of these forms very early on.

A more likely insertion in the later dicynodonts is on the medial side of the lower jaw into the intramandibular cavity between prearticular and surangular (figure 9: im.c.), which opens out laterally as the intramandibular fenestra (figure 6: i.fe.). The intramandibular cavity is approximately equivalent to the adductor fossa of *Dimetrodon* but it is more confined, and of course open laterally. In *Oudenodon* the cavity is rather narrow from side to side. However, it increases in volume anteriorly as it opens into the intramandibular fenestra. In this connection a deep scar on the dorsal surface of the angular that forms the ventral wall of the intramandibular fenestra could indicate the muscle attachment. Cluver (1975) reconstructs the posterior adductor inserting into this region of the lower jaw in *Chelydontops*, which he calls the adductor fossa. This is disregarded here because of the structure of the intramandibular cavity in *Dicynodon trigonocephalus*. The intramandibular fenestra is almost occluded by the lateral dentary shelf but the cavity contained within dentary, angular, surangular and prearticular is greatly expanded; indeed the medial surface of the surangular is excavated to extend the cavity and provide access to it from above. Such a cavity would provide too extensive an insertional area for a small muscle like the posterior adductor, although this might have inserted into the posterior part of the intramandibular cavity with the a.e.m. (figure 12: a.e.m., p.p.?). If this reconstruction is accepted then the two slips of the a..e.m constitute an extensive muscle pulling backwards, upwards and very slightly medially (figure 11).

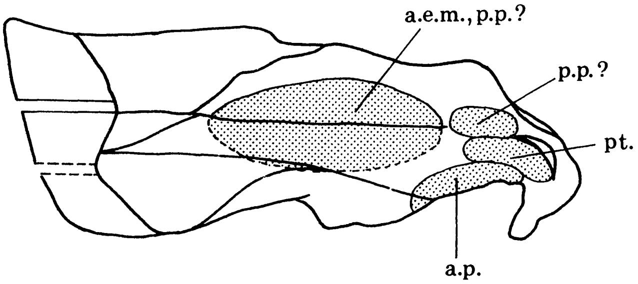


FIGURE 12. Diagram of the insertions of some of the principal jaw muscles. Medial view of the right side. (Half natural size.)

If the angle of insertion of the muscles on the lower jaw of *Dicynodon trigonocephalus* is determined, it is seen that, with the jaws open, the slips of the a.e.m. insert at an angle greater than 90° and that this angle becomes smaller, that is, approaches 90°, as the jaw closes. Similar considerations apply to the a.e.l., except that it is pulling more directly backwards and so inserts at a greater angle still than does the a.e.m., this angle reducing as the jaw is closed. Both muscles are therefore acting most effectively when the jaws are closed, indicating that the jaw muscles are operating on static pressure principles (Olson 1961) to produce a grinding or shearing mechanism.

As well as the lateral and medial external adductors, there is evidence for a posterior external adductor. In both *Oudenodon* and *Dicynodon* there is a pronounced muscle scar on the anterolaterally facing surface of the quadrate which would mark the origin of the muscle. As explained before, its insertion would be into the posterior part of the intramandibular cavity, or even further posterior, on the postero-dorsal corner of the medial surface of the surangular. This area is deeply pitted and striated in both *Oudenodon* and *Dicynodon*. The muscle would, in any case, be short and backward pulling, acting as a tie to stabilize the jaw joint.

The attachments of the internal adductors can be reconstructed with a fair degree of certainty (figures 10–13). The pseudotemporalis has already been discussed. The anterior pterygoideus takes origin from the ventrolateral palatal surface of the maxilla, the ectopterygoid and the lateral face of the quadrate ramus of the pterygoid, judging by the pattern of striations seen on these bones (figure 11: a.p.). It is usually reconstructed as inserting on the external surface of the lower jaw, beneath the articular condyle. To do this it must wrap around the ventral edge of the lower jaw ramus, posterior to the reflected lamina of the angular. In *Dicynodon trigonocephalus* this edge is a sharp keel, formed by the downgrowth of the prearticular and the angular. The jaw becomes smoothly rounded only relatively far back, near the retroarticular process. This smooth ventral margin bears striations and whorls, following the line of a ridge that starts on the lateral side of the ramus posteriorly and curves over to the medial side more anteriorly, where it peters out. On the medial surface the bone is also suggestively marked. It seems possible, then, that the anterior pterygoideus inserted mainly on the medial surface of the prearticular, turning onto the lateral jaw surface only far posteriorly (figure 12: a.p.). The muscle as reconstructed would pull forward, upward and medially.

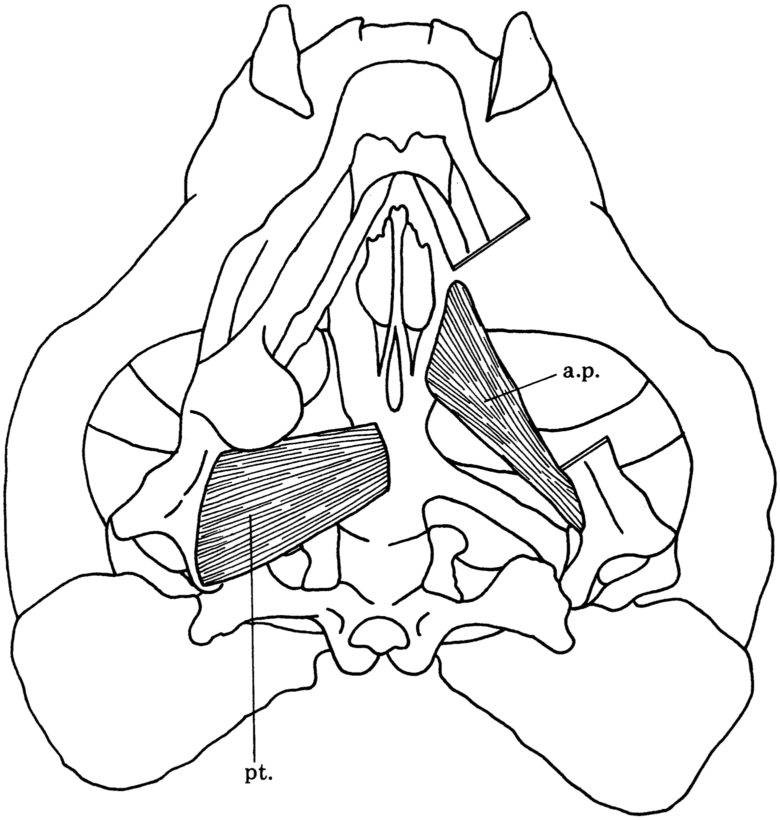


FIGURE 13. Palatal view of the skull and lower jaw to show the attachments of the pterygoideus musculature. The left ramus of the lower jaw has been cut through. (Half natural size.)

The posterior pterygoideus probably had its origin in the shallow fossae either side of the median pterygoid ridge on the palate (figures 10, 13: pt.). The muscle runs postero-ventrally and laterally to insert on the ventral surface of the median condyle, and possibly along the prearticular between the posterior adductor and anterior pterygoideus (figure 12: pt.).

The internal adductors are far less extensive than the external adductors. Both anterior and posterior pterygoideus muscles pull upwards and medially, although the dorsal component seems to be small. In addition the two muscles pull forward.

Another muscle is problematical. A small but prominent area of bone-marking is present on the antero-lateral surface of the maxilla postero-ventral to the caniniform process. Although close to an area that might have been horn-covered, the bone-marking in question forms a discrete patch much more in keeping with a muscle scar. It also extends onto the infra-orbital bar, which would rule out its indicating a horn covering. The scar is best shown on the *Oudenodon* specimens as *D. trigonocephalus* is damaged in this area. The area of marking stops short of the ectopterygoid, and seems therefore to be distinct from the scar relating to the origin of the anterior pterygoideus. If a muscle concerned with jaw closing were to originate from the maxilla, it would need to insert relatively far back on the lower jaw to permit a reasonable gape. One possibility might be that the muscle runs backwards and inserts into the tendon of the anterior pterygoideus, in which case it would be a more lateral slip of that muscle. Alternatively, the rest of the posterior part of the inner jaw surface is occupied by insertions of other muscles, but the maxillary muscle could insert on the lateral surface of the lower jaw. If it must insert relatively far back, then two possible sites are the reflected lamina of the angular (figures 6, 9: l.a), or the body of the angular below the lateral condyle (figure 6: b.a). The latter insertion would produce an almost horizontally running muscle when the jaw is closed which would be fouled by the overhanging surangular of the lateral condyle when the jaw is opened. This insertion is therefore unsuitable. A forwardly running muscle inserting on the reflected lamina or angular region has been proposed before in therapsids (Parrington 1955; Cox 1959) but is often now dismissed other than in the later cynodonts. However, it will be argued below that a strong forwardly pulling musculature would be necessary for the dicynodont masticatory cycle proposed, and additional evidence for a forwardly running muscle on the outer surface of the lower jaw is found in *Dicynodon trigonocephalus*. For such a muscle to run down and back to reach the reflected lamina the lateral dentary shelf must be attenuated just above and in front of the reflected lamina. In fact the lateral dentary shelf does diminish rapidly in this area, leaving a smoothly rounded access onto the lamina (figure 6: ac.). It is envisaged that the maxillary muscle would occupy most of the external lamina surface.

Three features of the dicynodont jaw muscle system are remarkable: first, the attachment of an adductor to the lateral surface of the zygoma; secondly, the considerable length and breadth of the temporal fenestra; thirdly, the lack of a coronoid process.

The lateral attachment of the adductor has led to the raising of the zygomatic arch, presumably to provide a longer fibre length. In fact, in terms of fibre length and muscle bulk, the lateral division of the muscle is much more extensive than the 'temporal' division. This would indicate that the evolutionary development of the dicynodont jaw adductors has taken a path quite different from the rest of the therapsids, where, according to Barghusen (1968), the primitive adductor had an origin from the temporal region, and this was elaborated before part of it developed into a zygomatic ('masseter') division. It would appear that the zygomatic division of the adductors in dicynodonts was an extremely early development and was present in forms as primitive as *Venjukovia* (Barghusen 1976).

Considering now the length and breadth of the temporal fenestra, increased length of the zygoma and the intertemporal bar obviously allows the fibre length of the adductors to be increased. It is generally supposed that flaring of the zygoma creates space that the bulky adductors can occupy. However, as reconstructed the a.e.l. would be almost entirely lateral to the zygoma, although it would bulge medially somewhat into the temporal fenestra on contraction. Also, the a.e.m. is not a particularly extensive muscle, and it would seem that not all of the temporal fenestra was occupied by muscle, and that an additional reason for lateral flaring of the zygoma exists. This might possibly be to allow the a.e.l. to have a definite lateral pull. The purpose of this could not have been to impart any lateral movement to the lower jaw because such movement is impeded by the tusks. However, all other adductors have some degree of medial pull, and it may therefore be necessary to balance these with a laterally pulling muscle, the a.e.l.

Another possibility remains: that the zygomatic arches may need to be laterally displaced as a consequence of the orbits becoming forwardly directed. Because of this forward direction, the postorbital bar must project laterally from the skull, and as the zygoma joins the postorbital bar it too is carried laterally. Although speculative, because of the uncertainty of the position of the eye, it is possible that *D. trigonocephalus* with its forwardly directed orbits had some degree of binocular vision. The reduced length of the snout aids this and also may imply that the sense of smell was somewhat reduced in importance, perhaps because sight was more important. This would in turn suggest that these dicynodonts, at least, occupied an open habitat or were nocturnal.

The absence of a coronoid process or eminence in dicynodonts is interesting. DeMar & Barghusen (1973) suggest that the development of a coronoid process in synapsids was initially to produce a backwardly pulling adductor muscle. The moment arm of such a muscle is increased over that of a near-vertically pulling muscle not inserted on a coronoid process. The initial selection for a backwardly pulling muscle and coronoid process in sphenacodonts and early therapsids might have been to prevent dislocation of the jaws when dealing with struggling prey. Dicynodonts must have lost the incipient coronoid process, inherited from sphenacodont ancestors, early on in their evolution, presumably when herbivory was adopted. However, DeMar & Barghusen suggest that there is another way to increase the moment arm of a muscle, though not one generally taken by the therapsids, and that is by increasing the distance of the insertion of the muscle from the jaw hinge. This would have the following consequences:

(1) encroachment of the musculature into the orbital region;

(2) anterior displacement of the orbits and anterior extension of the temporal fenestra;

(3) reduction of the relative length of the tooth row and modification of the relative position of the nares.

It is because of these consequences, DeMar & Barghusen suggest, that the alternative strategy of increasing the moment by development of the coronoid process, which leaves the posterior part of the jaw and the temporal fenestra unaffected, has been adopted by most therapsids. However, in dicynodonts the skull proportions are very different from those in other therapsids. There is a very short preorbital region and usually a long temporal fenestra. Even in *D. trigonocephalus*, a 'short-headed' form, the postorbital region is at least as long as the preorbital. Other selection pressures (concerning sight and olfaction) might be operating to select a relatively shortened snout region, but this is also the skull condition that would be expected to allow anterior migration of the adductor insertions. It is in fact seen that the powerful external adductors do all have their insertions concentrated in the anterior half of the lower jaw. The temporal fenestra has also extended forwards, another consequence (see (2) above) of the migration of the adductor insertions. In addition the length of the tooth row (see consequence (3) above) is modified in dicynodonts relative to other therapsids. The teeth of dicynodonts are reduced very early on in their evolution. Incisors are lost initially, then postcanines, as the horny beak and mouth plates are used to process food. Although the tooth row is short, propalinal movements of the jaws probably compensate for this (see §(iii) below).

Anterior expansion of the temporal fenestra has been accompanied by its posterior enlargement. This, together with the anterior migration of the adductor insertions, offers the possibility of decidedly backward-pulling muscles, even without the development of a coronoid process. Such as backward-pulling muscle force would be essential for the propalinal jaw movements outlined below.

The moment arm of the adductor musculature is therefore increased in a very different way in dicynodonts to that in other therapsids. Adoption of a different feeding strategy, based on a different system of jaw mechanics, is obviously a key innovation in dicynodont evolution.

(iii) *The masticatory cycle*

Most published accounts of dicynodont jaw function rely on the account given by Crompton & Hotton (1967) for *Emydops* and *Lystrosaurus*. Crompton & Hotton suggested that a unique feature of the dicynodont masticatory apparatus was antero-posterior movement, permitted by the specialized jaw hinge. They considered that food was processed only during retraction, protraction being merely a recovery stroke, and thus this did not constitute true propaliny, where food processing would occur during both protraction and retraction.

The present specimen of *Dicynodon trigonocephalus* sheds further light on the functioning of the jaws. Several unusual features of the upper and lower jaws need to be accommodated in any interpretation of dicynodont jaw function. The foremost of these is the unique dicynodont jaw hinge. It is obvious that it permits antero-posterior movement, as Watson (1948) pointed out. However, other features, for example, the extremely loose nature of the quadrate and quadratojugal attachment to the squamosal, the W-shape configuration of the jaw hinge, the shortness of the lower jaw, and the weakness of the pterygoid–quadrate connection, have not been given such detailed treatment. These will be discussed below.

In the specimen of *D. trigonocephalus* available, and also in the *Oudenodon* specimens, it is obvious that the quadrate is as free to move *post mortem* as is an element such as the stapes. In the acid-prepared *D. trigonocephalus* the quadrate and quadratojugal on each side slid away completely undamaged from the squamosal. No connection with the squamosal appears to exist, except that the dorsal edge of the quadratojugal is inserted into a transverse slit in the squamosal. In *D. trigonocephalus* the slit must have been extremely narrow and could have held no more than a thin film of the quadratojugal. The quadrate appeared to have rested in its recess in the squamosal without being suturally joined to it.

As the quadrate and quadratojugal have been removed in *D. trigonocephalus* the squamosal surface against which they rest is visible. The dorsal process of the quadrate fits into a deep fossa in the squamosal (quadrate recess) (figure 4: q.r.); the quadratojugal rests against a much shallower fossa (quadratojugal recess).

The quadrate recess has a roughened surface and bears many fine striations running along the length of the recess. The squamosal immediately above the recess is similarly marked, but the markings cease abruptly where the recess for the quadratojugal begins. The ventral margin of the quadrate recess is extremely thin. Its ventro-lateral corner is actually a contribution of the paroccipital process (figure 4: p.pr.). Although both paroccipital process and quadrate ramus of the pterygoid appear to be complete, the quadrate ramus does not reach the paroc-

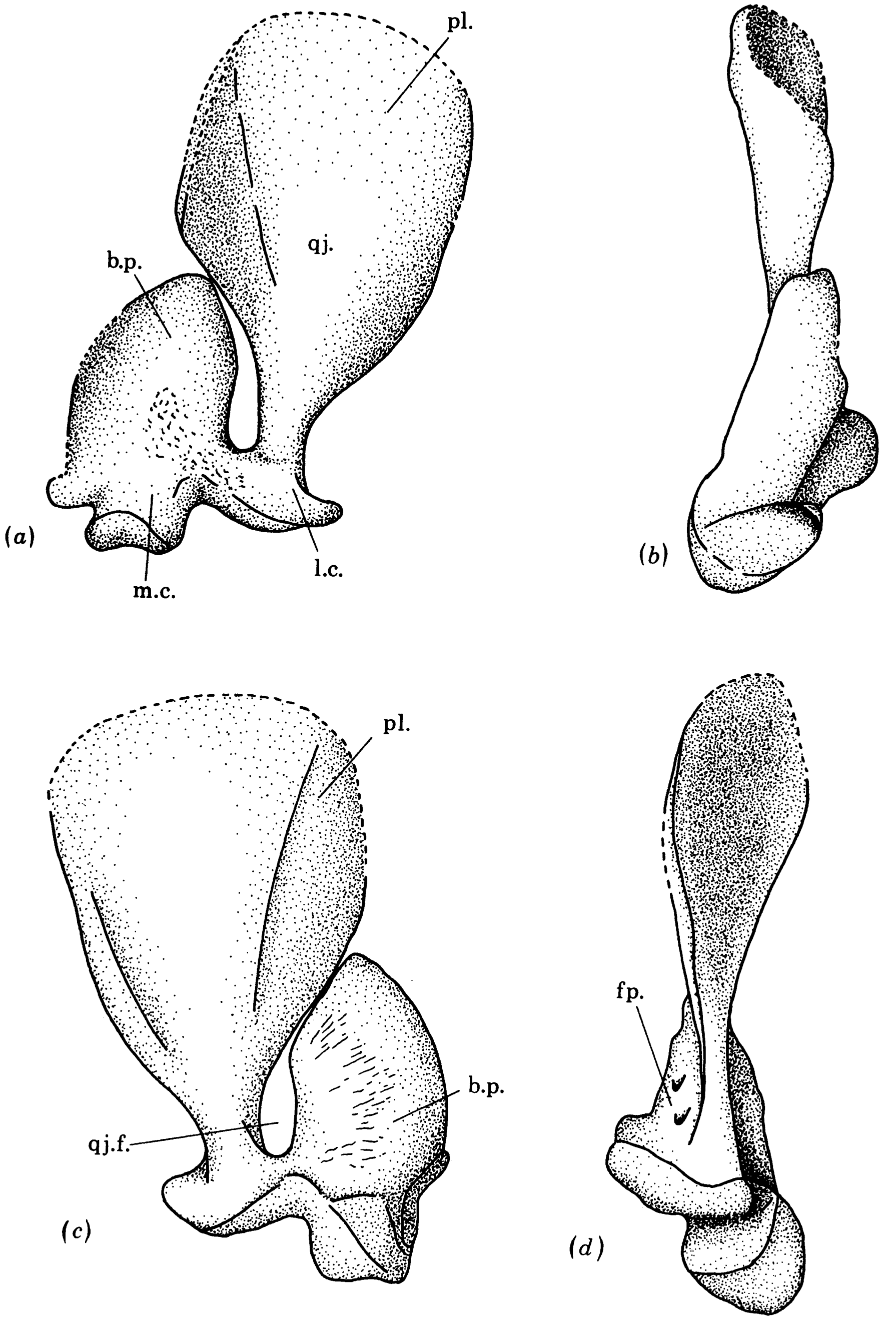


FIGURE 14. The left quadrate and quadratojugal (magn. × 1): (*a*) anterior; (*b*) medial; (*c*) posterior; (*d*) lateral. The broken line represents the reconstructed edge.

cipital process (figure 4: q.r.p.) but instead possibly abuts the medial surface of the quadrate condyle.

The surface of the quadratojugal recess is of extremely smooth bone, marked by fine striations on its lateral and ventral edges. The transverse slit in the squamosal, where the quadratojugal is presumed to have inserted, cannot be seen clearly.

The quadrate and quadratojugal show a high degree of detail (figure 14). The quadrate consists of a dorsal, bulb-like process, which expands ventrally to form the lateral and median condyles (figure 14: l.c., m.c.). The quadratojugal takes the form of a thin, fan-shaped plate of bone (figure 14: pl.), which constricts ventrally then expands to form a footplate which rests on the lateral quadrate condyle. A quadratojugal foramen, which is actually a short channel, is enclosed between the quadrate bulb and the quadratojugal plate (figure 14: qj.f.). The floor of this channel is deeply pitted and striated, and shows, posteriorly, two marked indentations, which are not foramina but might indicate some kind of ligamentous attachment.

The anterior surfaces of both quadrate and quadratojugal are reasonably smooth, bearing fine striations. The anterior surface of the quadrate also bears the muscle scar of the posterior adductor. The posterior surfaces of the two bones are quite different, however; the quadratojugal is again smooth and finely striated. However, the quadrate bulb is deeply striated over its complete surface apart from a smooth area just medial to the quadratojugal foramen. The striations, together with tiny pits, are of a high density, reminiscent of bone covered in horn, but the bone surface is generally more regular. When the condylar surfaces are examined microscopically it can be seen in damaged areas that underneath the superficial smooth and porous bone layer, the bone surface is very similar to that of the posterior quadrate surface. It might be, then, that the latter was also covered in cartilage. The posterior surface of the quadrate is smoothly convex from side to side, and also, more shallowly, dorso-ventrally. Together with a cartilage covering this shape would offer no hindrance to short-excursion movements in which the quadratojugal complex might be involved. The quadratojugal surface itself offers no indications of muscle or ligamentous connections and so presumably it too was fairly free to move in life. However, some constraint on movement must have applied. Judging from the relationship of the quadratojugal complex with the squamosal and the basicranial axis, and from specimens where the quadratojugal complex has 'slid', the postulated movement would be in an antero-ventral direction. This is expected because the complex is supported medially by the paroccipital process and posteriorly by the squamosal. Presumably though, there would be no actual bony connection to either paroccipital process or quadrate ramus of the pterygoid that would inhibit movement. This is seen in *Oudenodon*, where the quadrate ramus of the pterygoid merely fits in between the quadrate and the paroccipital process, and in *D. trigonocephalus*, where the quadrate ramus barely reaches the quadrate. The constraint to excessive movement in the antero-ventral direction, then, would presumably be muscular, from the posterior component of external adductors, and ligamentous, since it is possible that ligamentous tissue ran from the indentations in the quadratojugal foramen antero-dorsally up onto the anterior face of the squamosal. The short posterior adductor would also act as a tie to keep the jaw joint surfaces in contact as the quadrate moved. The importance of this movement in jaw function will be outlined below.

The lateral and median quadrate condyles in *D. trigonocephalus* are almost equal in size, in contrast to the situation in *Oudenodon*, where the lateral condyle is much the bigger of the two. The lower jaw condyles are also more nearly equal in size. As is usual in dicynodonts, the lower jaw condylar surface is extensive. It has an anterior portion composed of surangular and articular which is a single concave facet in which the median condyle plays no part. Posteriorly the lateral condylar surface is convex antero-posteriorly and concave from side to side. From its medial side is produced the convex (side to side and antero-posteriorly) median condyle. A profile of the articular condylar surfaces at this level is shown in figure 15*b*. The profile of the surfaces is a W-shape. This is matched by the profile of the quadrate condyles (figure 15*a*).

These two profiles would come into contact when the lower jaw is protracted. They form an extremely stable jaw joint, in which the articulatory surfaces can contact one another over a large area, even in extreme protraction and with the jaw open, when there is a risk of dislocation of the lower jaw. In addition this joint rules out relative transverse movement of the lower jaw.

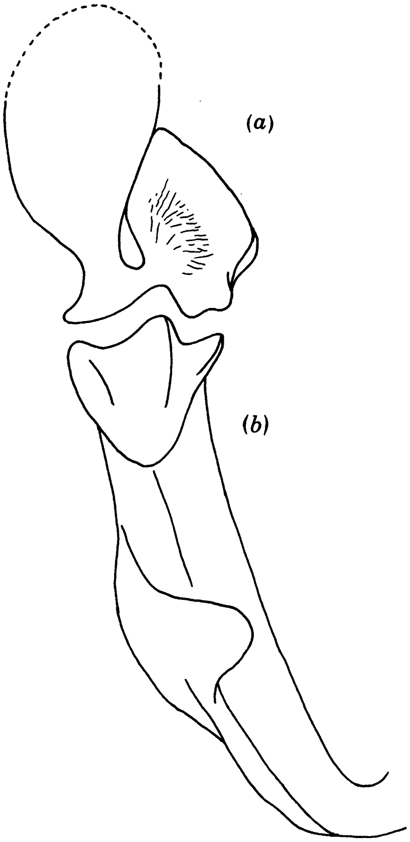


Figure 15. Diagram of the left jaw-hinge profile seen posteriorly: (*a*) the quadrate and quadratojugal; (*b*) the articular and lower jaw. (Approximately three-quarters natural size.)

This situation contrasts with that of the retracted position where the quadrate lateral condyle rests in the dish of the surangular–articular lateral condyle but the median condyles do not touch at all. This position is a very stable rest position with the jaw closed. However, if the jaw is opened in this position the articular surfaces quickly lose area-contact with one another and achieve only a line contact, becoming very unstable. Because of this situation, from consideration of the movable quadrate and the proposed muscle arrangement, the following masticatory cycle is suggested.

(1) From a closed-jaw, retracted position, the lower jaw is depressed and at the same time protracted. This carries the articular condyles into their posterior, stable contact. It also brings the upper and lower jaw beaks into contact, to cut and bite, when the jaws are closed again.

(2) The lower jaw is closed in the protracted position, enabling biting to occur at the beak. The main jaw closers are the a.e.m., a.e.l., the posterior adductor and the pterygoideus muscles.

The posterior component of the action of the external adductors must be partially counteracted by the forward pull of the internal adductors to prevent retraction of the lower jaw occurring automatically.

(3) The cutting action at the beak could be repeated by purely orthal movements of the lower jaw. Alternatively the lower jaw could be retracted while closed, in preparation for mastication of the food. This would take place between jaw surfaces posterior to the cutting edges and would involve a propalinal movement, food being masticated on the forward and on the back stroke.

(4) As the lower jaw goes from retraction to protraction during propaliny, various surfaces occlude: the anterior part of the longitudinal dentary groove (presumably with a horny covering) contacts the palatine, again probably horn-covered; also the premaxillary palatal ridge cuts into the median dorsal dentary groove. Food could presumably be effectively ground or crushed between these areas. However, this process leaves unused the posterior part of the longitudinal dentary groove, and the large anterior chamber formed by the domed ventral surfaces of the palatal premaxilla and maxilla. It seems, then, that the excursion of the lower jaw needs to be extended beyond that achieved solely by sliding of the articular on the quadrate, and this is possible by a small anteroventral movement of the quadrate. This brings into contact the posterior part of the longitudinal dentary groove and the palatines; at the same time the dentary tables can contact the palatal premaxilla surfaces. The anterior movement is stopped by the lateral surfaces of the jaw rami being wedged against the caniniform processes of the skull.

The excursion of the jaw between its anterior and posterior articulatory limits could continue indefinitely until the food was processed sufficiently, before the jaw was opened again. A well controlled and muscular tongue (see below) could manipulate the food, while a reptilian-type cheek (Cluver 1975; Crompton & Hotton 1967) would help to retain the food during processing.

The longitudinal excursion of the lower jaw has been referred to here as propalinal, in contrast to the suggestion of Crompton & Hotton (1967). It seems probable that in *Dicynodon trigonocephalus* there was an active forward stroke, as well as a back stroke, for the following reasons. The anterior pterygoideus muscle itself is a substantial forwardly pulling muscle. If a muscle also runs from the maxilla to the posterior lower jaw this would add to the forward muscle force, indicating that forwardly pulling muscles were involved in more than just a recovery stroke. Secondly, although the external adductors do have a backward component, in *D. trigonocephalus* this is not a particularly large part of the force, approximately 30 % of the vertical force, for the a.e.l. Furthermore, when the lower jaw is protracted, a strongly backward pulling muscle tends to brace the articular lateral condyle against the quadrate, rather than slide it backwards relative to the condyle. Conversely, moving the lower jaw forward requires much less effort because the quadrate moves back and down over the articular. It appears, then, that efficient forward movement of the lower jaw could be produced and used to comminute food material.

To summarize, *Dicynodon trigonocephalus* shows evidence of both forwardly and backwardly running adductor musculature. The jaw hinge is designed to permit propalinal movement, with a movable quadrate to increase the extent of jaw excursion. The jaw hinge also ensured maximum stability with a wide gape. The plant matter most suitable for this kind of apparatus, in an animal the size of *Dicynodon trigonocephalus*, might be the hard trunks of the large equisetalians.

(iv) *The reflected lamina*

The reflected lamina of the angular (figures 6, 8, 9) is a constant feature of therapsids and various uses have been postulated for it. Any explanation of its structure must take into account its three divisions: the lateral surface; the recess between the body of the angular and the lamina; and the medial surface of the lamina. Uses suggested for it to date include bearing a muscle on its lateral surface (Parrington 1955; Kemp 1969*a*), bearing muscles within the recess between the lamina and the body of the angular (Kemp 1972), and housing an air-filled chamber in connection with the hearing mechanism (Allin 1975).

The lateral surface of the lamina in gorgonopsids was thought by Parrington (1955) to bear an antero-dorsally running muscle attached to the zygomatic arch, which he called a masseter. Kemp (1969*a*) discusses the evidence for this, and concludes that, while the lamina did bear a muscle, the strengthening ridge on the lateral surface of the lamina suggests that the muscle runs postero-dorsally, attaching to the zygoma more posteriorly. This is called the zygomatico-mandibularis. However, the gorgonopsid reflected lamina is quite distinct from that of the dicynodont structure. Kemp (1969*a*) feels that it may even be independently evolved in the gorgonopsid line. In *Dicynodon trigonocephalus* the reflected lamina on each jaw is damaged but it can be seen clearly that the ventral edge of the angular is produced ventro-medially into a short triangular keel. This keel is continued more posteriorly by the ventral margin of the prearticular. The prearticular itself is unusual in that from its contact with the articular it spreads ventrally as well as anteriorly to overlap the angular keel. As stated, the latter is ventro-medially directed and has an extremely regular arc-shaped edge (figure 8: a.e.). The anterior margin of the keel and the ventral margin of the angular from which it originates are marked by a continuous shallow fossa (figure 9: sh.f.).

The reflected lamina is continuous along its antero-dorsal margin with the body of the angular and along its antero-ventral margin to the angular keel. The lamina curves ventro-medially under the ventral edge of the prearticular to follow the line of the angular keel. The narrow recess housed between the body of the angular and the lamina is open postero-dorsally and ventro-medially (figure 6: l.a.) although the postero-dorsal access is occluded by the surangular. There is a distinct notch (figure 6: n.) in the postero-dorsal edge of the angular lamina, where it leaves the body of the angular.

The lateral surface of the dicynodont lamina bears no obvious strengthening ridge, although it is finely striated over its entire area. The surface is crenulated and becomes more delicate posteriorly. Therefore no evidence of the insertion of a muscle like the gorgonopsid zygomatico-mandibularis is apparent. Furthermore, no muscle could run from the lamina to the zygoma because of the overhanging surangular.

However, in *D. trigonocephalus* it has been suggested (page 260) that the lateral surface of the lamina was occupied by the insertion of the forwardly pulling muscle whose origin was on the maxilla ('anterior adductor'). It is considered that, because of the very different structures of the dicynodont and gorgonopsid laminae, Kemp's (1969*a*) arguments are not applicable here.

Turning to the possible use of the angular recess for muscle attachment, Kemp (1972) reconstructs a pterygoideus muscle inserting in the recess in whaitsiid therocephalians. However, in *D. trigonocephalus* it has already been noted that the posterior pterygoideus did not encroach on any part of the lateral jaw surface (except for far posteriorly) but inserted on the posterior part of the prearticular, and the insertion of the anterior pterygoideus was entirely on the medial jaw surface.

In whatsiids Kemp further suggests that not only the pterygoideus muscle, but also a zygamatico-angularis muscle, inserted into the lamina recess. This latter muscle ran from the lamina to the postero-lateral internal side of the zygoma. A muscle in this exact position could not have been present in dicynodonts, because, again, it would need to first pass laterally to clear the overhanging surangular before continuing its medial passage to the zygoma. Indeed, no muscle inserting in the angular recess can comfortably pass postero-dorsally. This leaves the only direction of exit from the recess postero-ventrally and medially.

As far as the medial surface of the lamina is concerned, no interpretations have been given to date. In this analysis of the lamina in *D. trigonocephalus* the lateral surface of the lamina has so far possibly been accounted for. It is suggested that the other surfaces of the lamina were concerned with the throat and hyoid musculature, possibly relating to the presence of a muscular tongue. The reasons for this are as follows. The direction in which any muscle associated with the angular recess and medial surface would pull is down and backwards or medially; also the orientation and position of the lamina complex in *D. trigonocephalus* is suggestive of it being involved with support and control of throat structures: the lamina curves under the jaw ramus, to lie medial and ventral to it, almost at right angles to the vertical plane of the jaw ramus (figure 8: l.a). It therefore helps to reduce the large expanse between jaw rami, and between front and back of the jaws, which soft tissue must cover. It is postulated, therefore, that the medial side of the lamina might be occupied by a muscle, such as the inter-mandibularis, which would continue its insertion anteriorly along the body of the angular, perhaps to the dentary. There is a muscle scar in this region of the lower jaw, beginning on the anterior body of the angular, encroaching on the medial surface of the lamina. The fibres of the intermandibularis from each jaw ramus would meet medially, but some of the posterior fibres might attach to the hyoid apparatus, as do the mylohyoid fibres of mammals (Hiiemae & Jenkins 1969). Alternatively the muscle could grade into the constrictor colli posteriorly, as in chelonians and crocodilians (Schumacher 1973).

Another possibility is that digastric musculature (not necessarily primarily for opening the jaw) occupied part of the lamina, running to the hyoid apparatus. There is reason to believe that the hyoid apparatus was fairly extensive in dicynodonts (Owen 1860).

Turning to the angular recess, a candidate for insertion here is the branchio-mandibularis. This muscle inserts on the medial side of the angular and sub-angular in chelonians, but in crocodilians it inserts more laterally on the angular surface. It arises lateral to the hyoid, running forward and laterally to its insertion, which means that in dicynodonts it could easily pass over the body of the angular into the angular recess. However, the problem remains that the angular recess in *D. trigonocephalus* is a substantial, if narrow, cavity. In crocodilians the branchio-mandibularis is a fairly small muscle, and reasons for its possible elaboration in dicynodonts are obscure. The hyoid skeleton is implicated in throat movements involved in feeding and breathing. It is not impossible, then, that muscles connected with it, like the branchio-mandibularis, became important and elaborated in therapsids, but the present specimen does not offer any evidence of this.

A completely different use has been attributed to the reflected lamina by Allin (1975), who considers that the angular recess housed an air-filled chamber which extended onto the external surface of the body of the angular. Thin tissues superficial to the air-filled chamber acted as an ear drum. Sound vibrations were transmitted from the reflected lamina (which was functionally part of the ear drum) to the stapes, via the mandible and quadrate. For certain reasons this does not seem acceptable in dicynodonts. The angular recess in dicynodonts forms only a part of the entire reflected lamina complex: much of the lamina, especially the posterior and ventral margins, does not surround the recess, but is a free-standing surface. It is, however, far too thick to constitute part of a tympanum. Also, if the reflected lamina and recess are part of the auditory apparatus, the striations and crenulations on the bone become difficult to explain. Apart from these anatomical observations, it is doubtful whether vibrations could have passed at all effectively in the way outlined. The tympanum is said to be held by the angular: the reflected lamina in fact becomes part of the tympanum. However, the angular is also expected to play the role of ossicle to transmit the vibrations to the quadrate. In any case, it is doubtful whether vibrations in the air of the chamber in the recess would actually be transmitted to the body of the angular at all. This is so massive that the vibrations would be more likely to be reflected. The quadrate also is a bulky bone, although only loosely attached to the skull. It must also be remembered that the propalinal movements of the lower jaw would cause considerable vibrations at the jaw hinge and at the masticatory surfaces, which must have interfered with hearing if the auditory apparatus was as Allin suggests. Presumably dicynodonts would spend most of their time feeding, as most herbivores do, and so the interferences of feeding with hearing would be significant.

Other forms of auditory apparatus have been proposed for dicynodonts. Cox (1959) suggested a tympanum behind the quadrate reached by an extra-stapes. Barry (1968) suggested that the hyoid apparatus transmitted sound to the stapes. It would seem, however, that normally the hyoid apparatus would be surrounded by the muscles of the throat and jaws, which would damp out any vibrations before they could be passed effectively to the stapes. The repeated observations of the hyoid apparatus associated with the stapes may reflect its need for a firm anchorage, if it does indeed bear the origin of tongue or throat muscles. The stapes is a very robust bone considering its role in sound conduction, and it is possible that this was not its only role, as Camp & Welles (1956) point out in *Placerias*. It may have braced the quadrate, and, as suggested, have supported the hyoid bones to which the throat muscles attached.

In conclusion it appears that the reflected lamina of the angular and of the angular recess could have been sites of the insertions of the following muscles: the anterior adductor, the intermandibularis and possibly the digastric, and the branchio-mandibularis.

(v) *The nasal capsule*

There are few accounts of the nasal region of dicynodonts, those of Pearson (1924*a*), Watson (1960) and Cluver (1971) being the most comprehensive. In *D. trigonocephalus* the left side of the snout is broken off in the midline and through the zygomatic arch. Since the skull roof is also missing in this area it is possible to see certain structures of the dorsal palate and nasal capsule (figure 16).

A very short premaxillary channel runs from the anterior edge of the internal choana almost directly dorsally to terminate just posterior to the point at which the median ridge of the premaxilla arises (figure 16*b*: p.cha.). The surfaces of the channel are finely pitted. Cluver (1971) considered that a similar channel in *Lystrosaurus* carried the duct of Jacobson's organ to the internal choana.

A large cavity formed in the maxilla and jugal of the infraorbital bar is present. It opens on its medial side into the nasal capsule. The root of the canine tusk (figure 16*b*: r.c.t.) protrudes into this maxillary–jugal cavity (figure 16*a*, *b*: m.j.c.). Just posterior to the cavity, the palatine

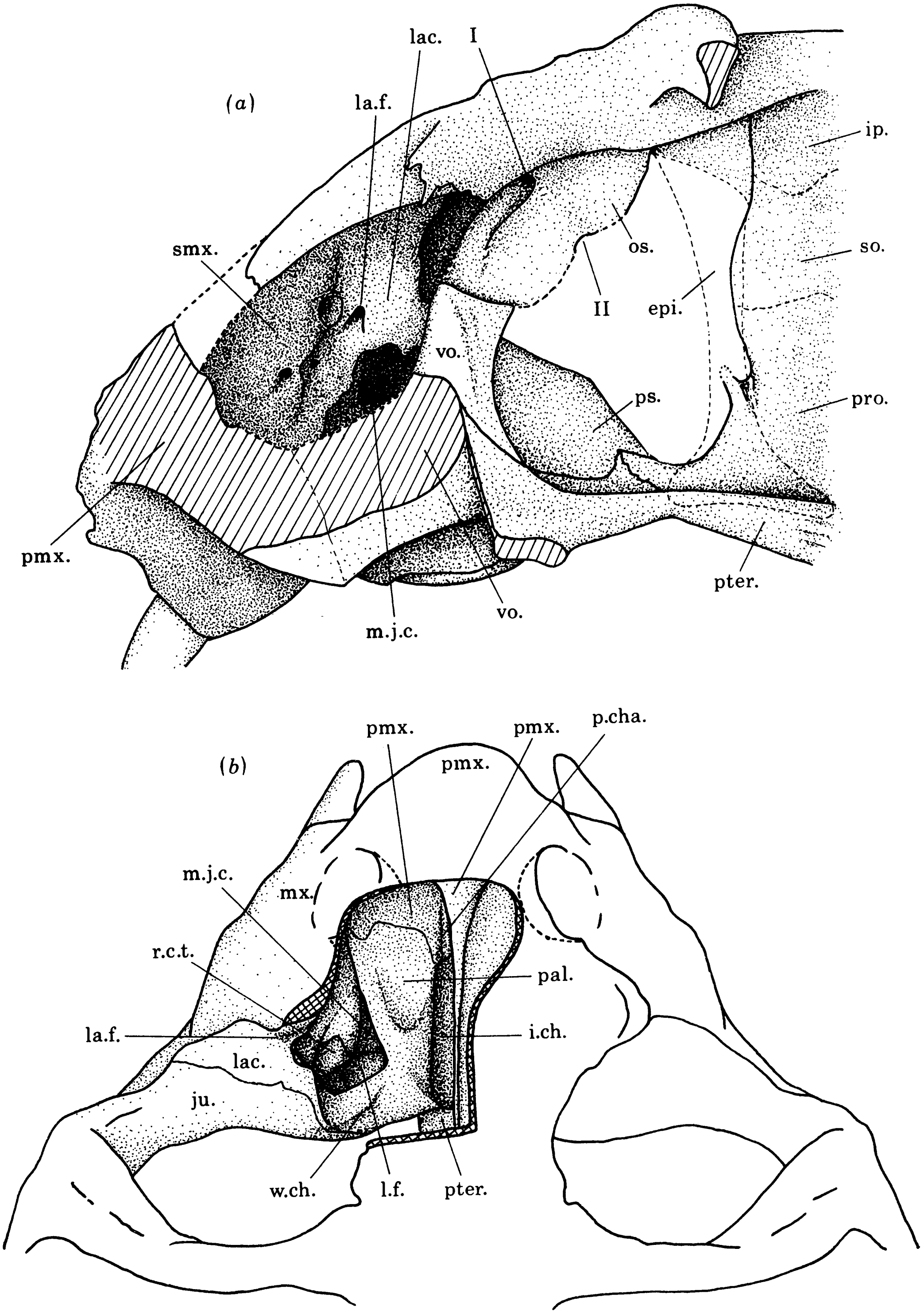


FIGURE 16. (*a*) The septomaxilla, nasal capsule and orbitosphenoid complex of the left side. The postorbital bar has been removed and the snout is broken away on the midline through vomer and premaxilla. Cross-hatching indicates a broken surface. (Natural size × *ca.* 0.83.) (*b*) The dorsal palatal surface showing the left maxillary–jugal cavity and posterior nasal capsule. Part of the skull roof has been removed. Cross-hatching indicates broken or cut edges. The position of the septomaxilla recessed within the nostril is shown by a broken line. On the left side it has been cut through. (Two-thirds natural size.)

of the infraorbital bar is deeply notched and bears a wide channel which runs antero-medially into the nasal capsule (figure 16*b*: w.ch.).

The maxillary–jugal cavity has been called the maxillary antrum by Watson (1960) and by Cluver (1971). It is doubtful whether this is homologous with the maxillary antrum of mammals; hence the choice of a non-committal name here. Various uses have been proposed for this cavity. Cluver concludes that it is only incidentally concerned with housing the canine tusk. Watson supposed that it contained a diverticulum of the respiratory passage. Another possibility is that it contained a venous sinus. Cluver discusses the labial fossa in *Lystrosaurus* and concludes that it transmitted blood vessels into the snout. In *D. trigonocephalus* the labial fossa communicates with the maxillary–jugal cavity, and so might have represented the vessels draining a sinus in the cavity.

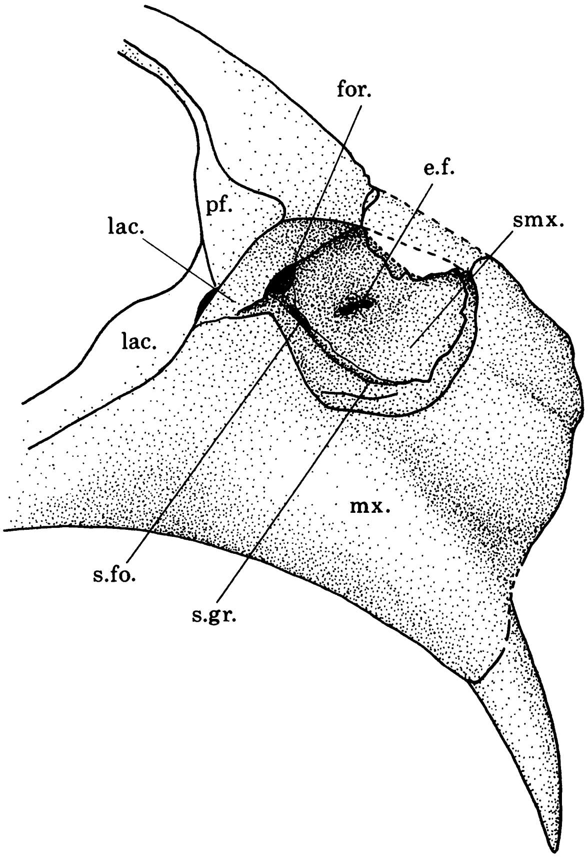


Figure 17. The septomaxilla in right lateral view. (Natural size × *ca.* 0.83.)

Compared with other therapsids or primitive mammals the dicynodont snout is extremely short, but fairly wide. However, it is unlikely that the same relative volume is available in the snout for an extensive nasal epithelium, and this might lend more weight to Watson's suggestion that the maxillary–jugal cavity was an accessory olfactory surface, except that long-snouted therapsids also possess such cavities. Also, the cavity is very definitely walled-off antero-medially by the maxilla so that any accessory olfactory surface would be relatively isolated from the main olfactory surface. Also there would presumably need to be a separate duct or tube into the internal choana, or else a rather elaborate connection between main and accessory surfaces.

The septomaxilla (figure 17: smx.) is a saucer-shaped bone orientated on edge in the external naris. Postero-dorsally the septomaxilla contacts the lachrymal and between the junction of lachrymal, septomaxilla and maxilla a large foramen (figure 17: for.) is seen. This leads into a wide groove (figure 17: s.gr.) in the maxilla, running antero-ventrally. This groove is perforated by a smaller foramen (figure 17: s.fo.) about 3 mm antero-ventral to the first. The septomaxilla itself has irregularly crenulated edges and is marked by striations radiating from its centre, near to which is a small, elongated foramen (figure 17: e.f.). The medial surface of the septomaxilla can be seen, as the left side of the snout is broken away (figure 16*a*). The internal openings of the three foramina can be seen clearly. Also the internal opening of the lachrymal canal, a small foramen in the medial surface of the lachrymal facing antero-ventrally and medially, is easily seen (figure 16*a*: la.f.). At its antero-ventral edge this foramen opens out into a fan-shaped trough bordered by distinct ridges. The posterior opening of the lachrymal canal is a small foramen, deeply recessed in the lachrymal, which bone forms the anterior edge of the orbit (figure 2: la.f.).

The presence of turbinal bones has been suggested in various therapsids by Kemp (1969*a*). In *Lystrosaurus*, Cluver (1971) describes ridges on the ventral surfaces of the nasals and frontals, which he concludes either supported cartilaginous sphenethmoidal commissures or else supported a pair of turbinals in a posterior extension of the nasal cavity. In *Dicynodon trigonocephalus* the ventral surface of the skull roof is prepared, and, although somewhat damaged, shows no clear indication of ridges similar to those in *Lystrosaurus*. In the *Oudenodon* specimens the ventral surfaces of the frontals and nasals have been prepared and here again there are no definite ridges.

Kemp (1969*a*) suggests that the naso-frontal ridges in *Kingoria* (and presumably this would apply to *Lystrosaurus*) are connected with support of turbinals, and finds it ‘not at all surprising in synapsids that the enlargement of the snout should lead to it being developed as an olfactory organ, and that it should be advantageous to enlarge the surface area of the olfactory epithelium by the development of conchae or turbinals.’ However, this suggestion may be of only limited application to most dicynodonts, since it is suggested in the present work that along with reduction of the snout went a reduced olfactory sense (page 261). The naso-frontal ridges in dicynodonts would then perhaps receive a cartilaginous connection of the mesethmoid, and the extent of this connection might vary from form to form, accounting for the variable occurrence of the ridges.

(vi) *The cranial nerves and blood vessels*

Dicynodon trigonocephalus exhibits most of the foramina and notches described by other authors (for example: Cox 1959; Cluver 1971) in connection with the cranial nerves and blood vessels. On the occipital surface (figure 18) the jugular foramen allows passage of nerves IX, X and XI and the posterior cerebral vein from the braincase; according to Cox, the post-temporal fenestra (figure 18: p.t.f.) transmits the vena capitis dorsalis and the channel between stapes and paroccipital process transmits the vena capitis lateralis (figure 18: v.c.l.); the quadratojugal foramen may have transmitted the mandibular vein. On the palate (figure 3) the internal carotid artery enters the braincase through a foramen on the pterygoid–basisphenoid suture (figure 3: i.c.). Anterior to this a small foramen transmits the palatine branch of nerve VII (figure 3: p. VII), which leaves the braincase at the point of the notch for the geniculate ganglion, through the basisphenoid. A foramen in the parasphenoid–pterygoid suture on the lateral surface of the median septum indicates the exit of this nerve from the basisphenoid-parasphenoid complex. Further forward the palatine nerve passes through an ectopterygoid foramen and emerges ventrally at the lateral palatal fenestra (figure 3: l.p.f.). The branches of nerve V are presumed to exit from the braincase at the prootic incisure (figure 4: p.i.). The orbitosphenoid complex shows the foramen for the exit of nerve I from the braincase (figure 16: I), and the notch for the passage of nerve II (figure 16: II).

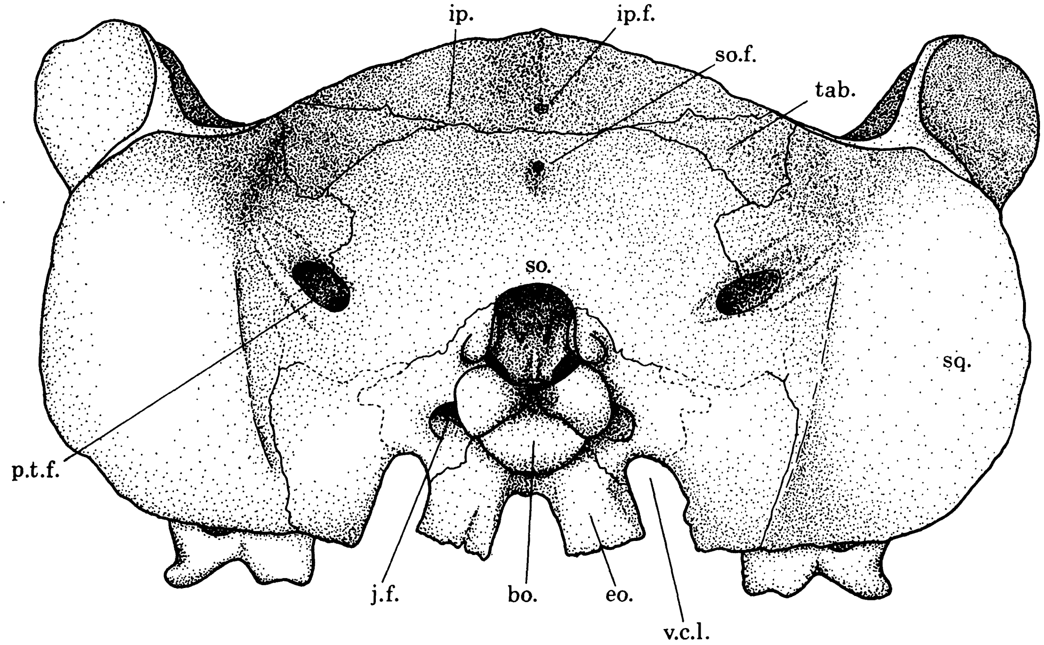


Figure 18. Occipital view of the skull. (Two-thirds natural size.)

In addition to these foramina and notches, *D. trigonocephalus* bears on the occiput two midline foramina: one near the dorsal margin of the supraoccipital (figure 18: so.f.); the other near the ventral border of the interparietal (figure 18: ip.f.). A further two foramina are present in the sidewall of the braincase. The interparietal has an exposure on the sidewall of the braincase above the supraoccipital, which it overlies (figure 4). Within this overlap lies a medium-sized foramen. A bristle passed through the median supraoccipital foramen emerges here, or through the similarly placed foramen of the contra-lateral side of the skull (figure 4: so.f.). Anteriorly, the interparietal is overlain by the down growing sheet of parietal, which emerges from beneath the postorbital. Anterior to the parietal the mesethmoid–orbitosphenoid complex is found. Between its posterior edge and the anterior edge of the parietal, a medium-sized foramen is present (figure 4: m.f.).

Between these various notches and foramina the paths that the nerves and blood vessels take are highly conjectural except where grooves or bone markings indicate the presence of these soft structures. Using grooves on the prootic, Cox (1959) was able to arrive at a scheme for the organization of some of the head veins in *Kingoria*. Cluver's description of the head veins of *Lystrosaurus* (1971) shows a similar organization.

The vena capitis dorsalis is presumed to have entered the skull through the post-temporal fenestra. A groove (figure 4: gr.) on the prootic of *D. trigonocephalus* indicates that, before entering the braincase, this passed medially and slightly dorsally from the post-temporal fenestra. However, the point of entrance to the braincase cannot be seen in the present specimen.

The vena capitis lateralis passed through the channel between stapes and paroccipital process. From here, in *D. trigonocephalus* a well marked groove runs to the prootic incisure, presumably indicating the path of the vein. There is no obvious evidence of a connecting vessel between the dorsal and lateral head veins.

Evidence of other vessels is given by the midline supraoccipital and the supraoccipital–interparietal foramina in *D. trigonocephalus*. It is unlikely that a single vein ran straight through the channel so created from occiput to lateral surface of the braincase. Possibly the side-wall foramen represents the exit from the braincase of a vein draining the transverse sinus which might be a branch of the vena capitis dorsalis. The supraoccipital foramen could indicate the exit of the occipital vein, which drains the longitudinal sinus of the braincase.

The forelimb and pectoral girdle

(i) *General*

The girdle is represented by both scapulae, fairly complete but distorted, the right clavicle, which is again fairly complete but has surface damage, the right coracoid and procoracoid and fragments of these elements from the left side, and part of the interclavicle and sternum. No cleithrum was preserved, if indeed it was present in life (see Cox (1959, p. 340) for a discussion). The forelimb is represented by the left humerus, ulna and radius, all in good condition, and several elements of the right manus.

Before preparation the pectoral girdle was in association with vertebrae 4 to 8. Watson (1960) reconstructs the scapula lying adjacent to vertebrae 5 and 6, but in the present reconstruction (figure 44) it has been placed more posteriorly.

(ii) *Humerus and pectoral girdle*

To assess the distortion and damage of TSK 14, reference was made to two other well preserved but unidentified dicynodont specimens of a similar size. These were TSK 68 and TSK 37. The humerus has needed little reconstruction (figure 19). It is a robust rod of bone, having its distal end expanded antero-posteriorly and its proximal end expanded antero-ventrally to form the massive delto-pectoral crest (figure 19*c*: d.c.).

The distal half of the bone is a flattish triangular plate. The ventral surface is pierced by the antero-laterally directed entepicondylar foramen. There is no ectepicondylar foramen. The surface of the distal end of the bone encroaches on the ventral surface, forming a facet for the proximal end of the ulna (figure 19*c*, *f*: ul.f.). The facet for reception of the proximal end of the radius (figure 19*c*, *f*: rad.f.) is more anterior.

The proximal half of the humerus seen dorsally bears the head of the bone (figure 19*c*, *d*: h.) on its antero-medial margin, from which the delto-pectoral crest descends as a robust plate, forwardly directed. Its antero-ventral edge is thickened distally and bears many pits and striations. The posterior margin of the proximal part of the humerus bears a marked oval rugosity (figure 19*d*: rug.), not unlike that for the triceps origin on the scapula.

Since the head was incompletely ossified it was necessary to reconstruct this to be able to assess the possible movements of the humerus. The area of the bone where the head arises is clearly marked by rugosities and unfinished bone. This area is mostly dorsally facing, and therefore the reconstructed head faces dorso-medially.

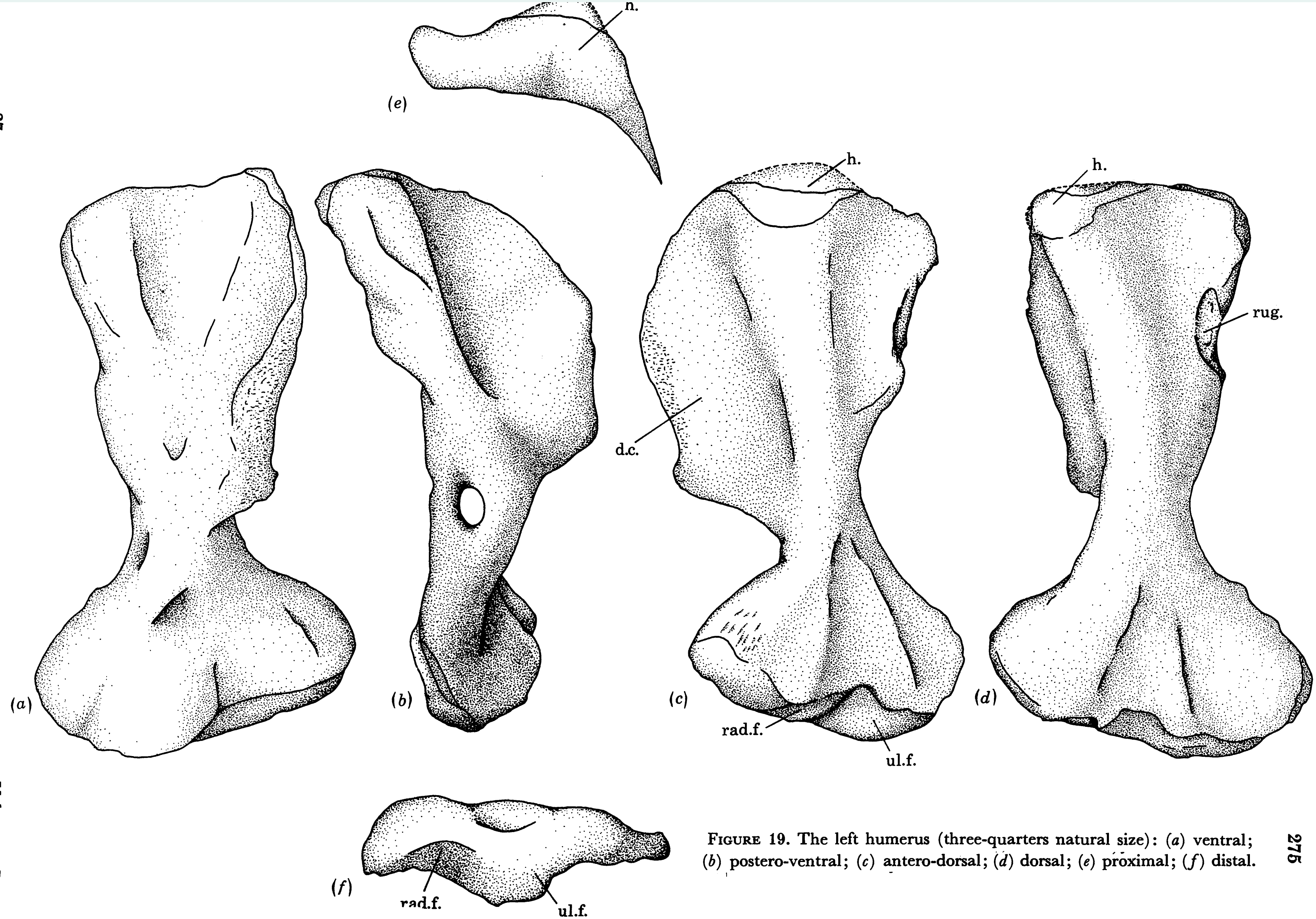


FIGURE 19. The left humerus (three-quarters natural size): (*a*) ventral; (*b*) postero-ventral; (*c*) antero-dorsal; (*d*) dorsal; (*e*) proximal; (*f*) distal.

The scapula of TSK 14 needed considerable reconstruction. The scapula is a thin, fan-shaped blade of bone constricted and thickened below the acromion process into a stout column. The column then broadens out again to carry, on its postero-ventral side, the scapula contribution to the glenoid articulation (figure 20). Where the thickened posterior edge of the blade merges into the stout column, a distinct raised, oval, roughened area is present (figure 20*c*: rug.). This takes the form of a central mound surrounded by an oval trough, the surface of which is pitted and striated. The roughened area faces posteriorly and a little laterally. Cruickshank (1967) describes a 'knob' in this position in *Tetragonias* and concludes it to be the origin of the triceps muscle.

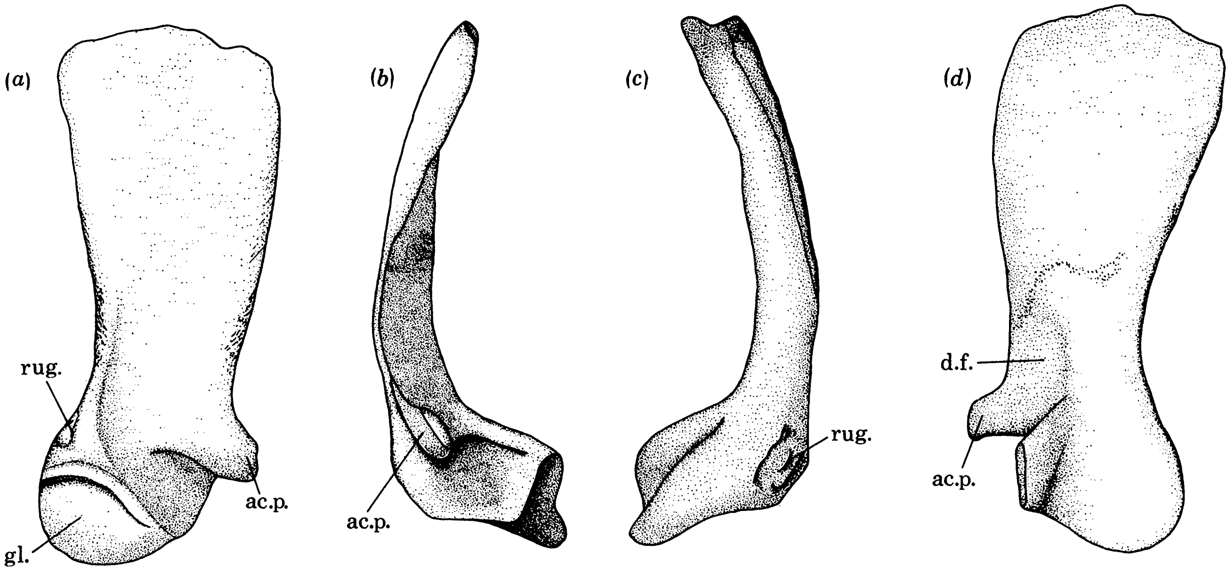


FIGURE 20. The left scapula (three-fifths natural size): (*a*) lateral; (*b*) anterior; (*c*) posterior; (*d*) medial.

In neither case, left or right, was the glenoid complete. Also the neck of bone that bears the glenoid, below the blade of the scapula, was bent under the blade, as numerous cracks and 'faults' in this area show. When this distortion is corrected for, however, the clavicle may be articulated with the acromion process. The clavicle is a rod of bone with both ends somewhat expanded and orientated at right angles to one another (figure 21). The medial end is expanded into a spoon-shaped surface that lies ventral to the surface of the antero-lateral wing of the inter-clavicle (figure 21*d*: sp.).

The distal end is expanded dorsally into a fan-shaped plate (figure 21*a*: d.e.). The dorsal and dorso-lateral edges of this plate make contact with the acromion process of the scapula. When in articulation with the acromion the clavicle lies at an angle of approximately 35° to the horizontal and the glenoid faces outwards and backwards. The scapula blade is almost vertical. The orientation of the clavicle at an angle to the horizontal is borne out by the interclavicle. This has been reconstructed as a rectangular bone with the anterior edge longer than the posterior (figure 22*a*–*c*). The posterior edge is slightly convex. The outer three edges are concave. Viewed from the ventral side the interclavicle consists of two plates of bone meeting in the midline to form an angle of approximately 120° dorsally (figure 22*a*). Where the plates meet posteriorly, the bone is drawn up into a very pronounced boss (figure 22*a*, *c*: b.), which therefore projects ventrally. This falls away quickly on the posterior side to leave a rather thin posterior edge.

Both coracoid and procoracoid (figure 23) are flattened bones which lie in a plane at an angle to the interclavicle, the lateral edges being more dorsal than the medial edges. The procoracoid (figure 23*a–c*) is almost pentagonal, with the longest edge placed posteriorly. The lateral half of the posterior edge and the lateral edges are thickened. These thickenings form the articulation with the scapula and part of the glenoid, respectively (figure 23*c*: sc.a. and gl.). In contrast, the anterior and medial edges are attenuated. The anterior edge rests comfortably over the ventral surface of the clavicle and the medial edge just contacts the interclavicle. The diminishing thickness of the anterior edges of the procoracoid and the convexity of the medial end of the clavicle create a well fitting, overlapping joint.

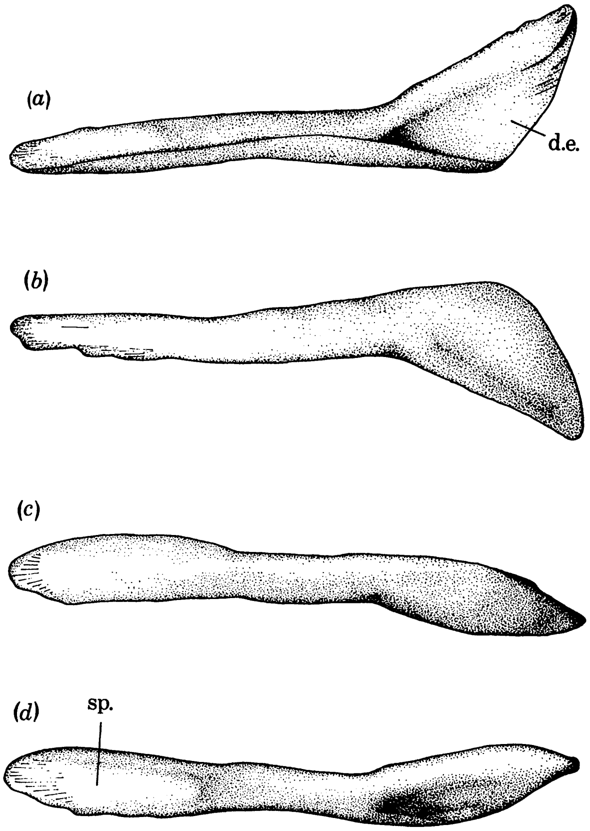


FIGURE 21. The right clavicle (three-fifths natural size): (*a*) posterior; (*b*) anterior; (*c*) ventral; (*d*) dorsal.

The coracoid (figure 23*d–f*) contacts the posterior edge of the procoracoid by means of its straight anterior edge. The lateral edge of the coracoid is expanded into a rounded boss which forms part of the glenoid (figure 23*e*, *f*: c.). The coracoids of each side do not appear to be wide enough to meet the interclavicle medially, except by a cartilaginous connection.

As noted above, the glenoid faces backwards and outwards, and the scapula blade is almost vertical and thrown very slightly forwards, but not to the degree suggested by Watson (1917).

The shape of the glenoid is interesting (figure 24). The planes of the scapular and coracoid surfaces of the glenoid meet at an angle of 80 to 85°. Neither surface is flat. The scapular facet bears a marked semicircular groove over the dorsal half of its surface (figure 24*a*: s.g.). Below this the facet swells out into a low subcircular convexity, which continues to the edge of the scapular facet, where it abuts the coracoid facet (figure 24*a*: s.c.). The latter also bears a shallow fossa, roughly triangular, in the centre of its surface, the base of the triangle running from the posterior edge of the facet (figure 24*a*: tr.). Medial to this fossa the coracoid facet swells into a low convexity which meets that of the scapular facet (figure 24*a*: l.cv.).

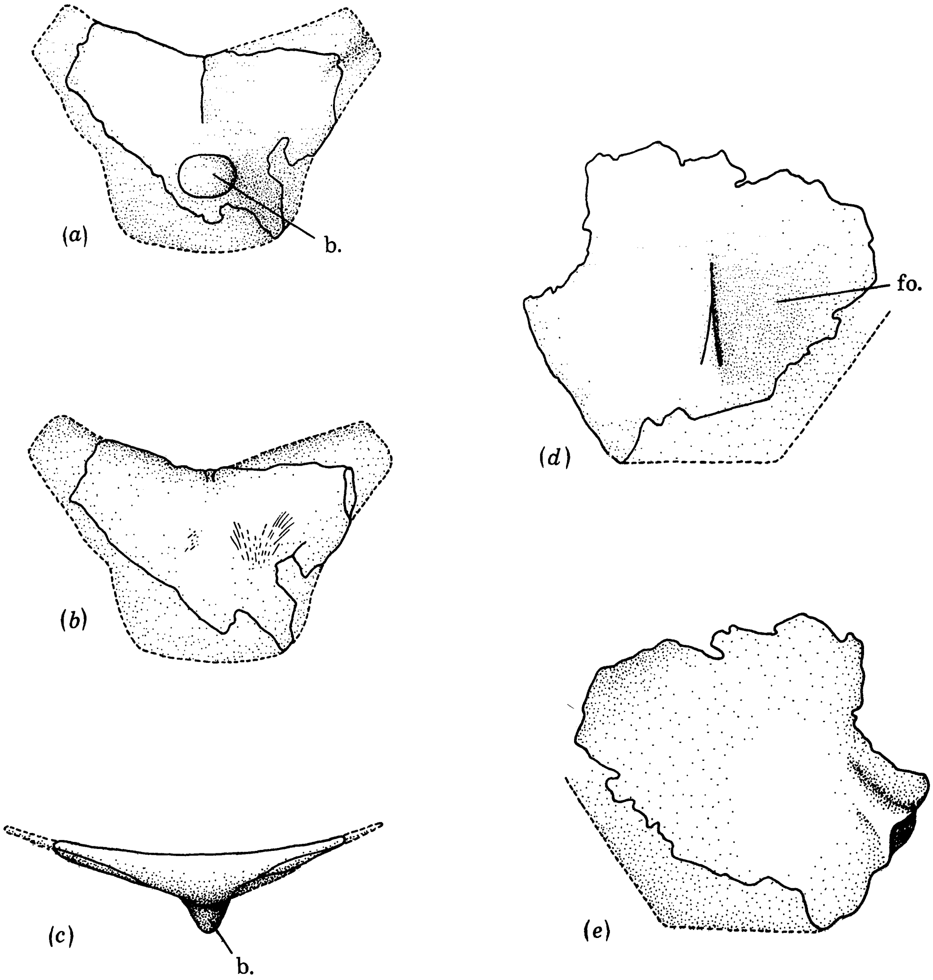


FIGURE 22. (*a*)–(*c*) The interclavicle (three-quarters natural size): (*a*) ventral; (*b*) dorsal; (*c*) anterior. (*d*), (*e*) The sternum (three-quarters natural size): (*d*) ventral; (*e*) dorsal.

When the humerus is articulated in the glenoid, the dorso-medial surface of the head is in contact with the semicircular scapular groove. The ventral surface of the humeral head is concave from anterior to posterior. It also slopes gently dorso-laterally, making it congruent with the surface of coracoid facet bearing the triangular fossa. The ventral surface of the head may slide over this area of the coracoid facet without losing contact, as the humerus is swung forwards and the dorsal head is rotating against the scapular facet of the glenoid. The humerus is in a typical sprawling position, at right angles to the body. The delto-pectoral crest makes an angle of approximately 80° to the horizontal. The humerus has a limited amount of movement.

It can be retracted approximately 15° and protracted approximately 35° from the lateral orientation. When the head is articulated as indicated previously, some long axis rotation is possible. The humerus may rotate anticlockwise on the left hand side, which forces the antebrachium back, or the body forward if the antebrachium is anchored. A smaller degree of clockwise rotation is also possible. This forces the antebrachium forward, but the posterior edge of the humerus soon abuts the glenoid edge, stopping the movement.

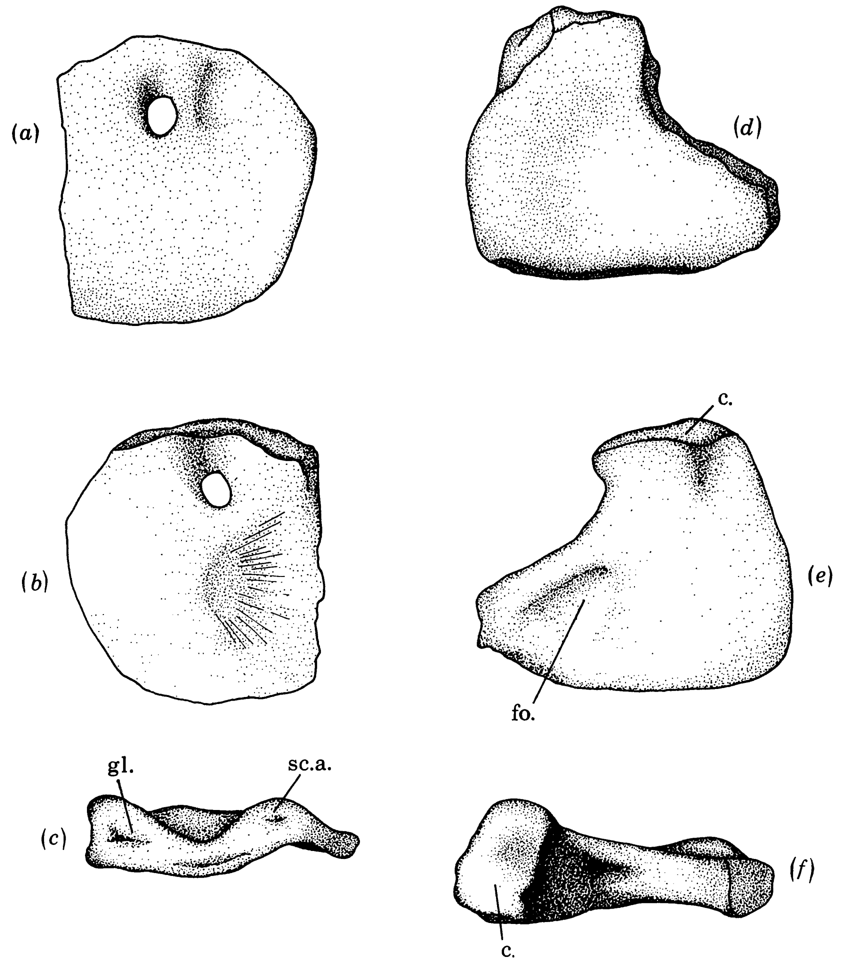


FIGURE 23. (*a*)–(*c*) The right procoracoid (three-quarters natural size): (*a*) ventro-lateral; (*b*) dorso-medial; (*c*) lateral edge. (*d*)–(*f*) The right coracoid (three-quarters natural size): (*d*) dorso-medial; (*e*) ventro-lateral; (*f*) lateral edge.

The length of the movement arc might be increased if part of the shoulder girdle were free to move about the rib cage. This might be possible in *D. trigonocephalus*. The articulation of the proximal end of the clavicle and the interclavicle is fairly free. The spoon-shaped end of the clavicle fits comfortably under the interclavicle facet and is able to pivot about that facet. The distal end of the clavicle moves posteriorly or anteriorly with a negligible medial component. If one assumes a strong connection between the scapula and the clavicle (both the acromion process and the proximal end of the clavicle are deeply striated, suggesting strong ligmentous connections), and also between the interclavicle, sternum and the anterior ribs, then a muscle originating from the rib cage could pull the scapula, and indirectly the clavicle, backwards (and medially), the clavicle pivoting about the interclavicle. The glenoid would also obviously be carried backwards, and with it the humerus, so extending the posterior limit of the limb movement. The need for a firm clavicle-scapula attachment would explain the well developed acromion process and the well fitting clavicle. Also it could explain the failure of the coracoids to meet the interclavicle in the midline, as this would prevent pivoting of the clavicle.

The muscle to effect this postero-medial movement of the scapula would need to insert on the dorsal, posterior edge of the scapula blade and run to the stout ribs of the anterior thoracic region. The serratus superficialis anterior occupies this region and could perform the role of rotating the glenoid.

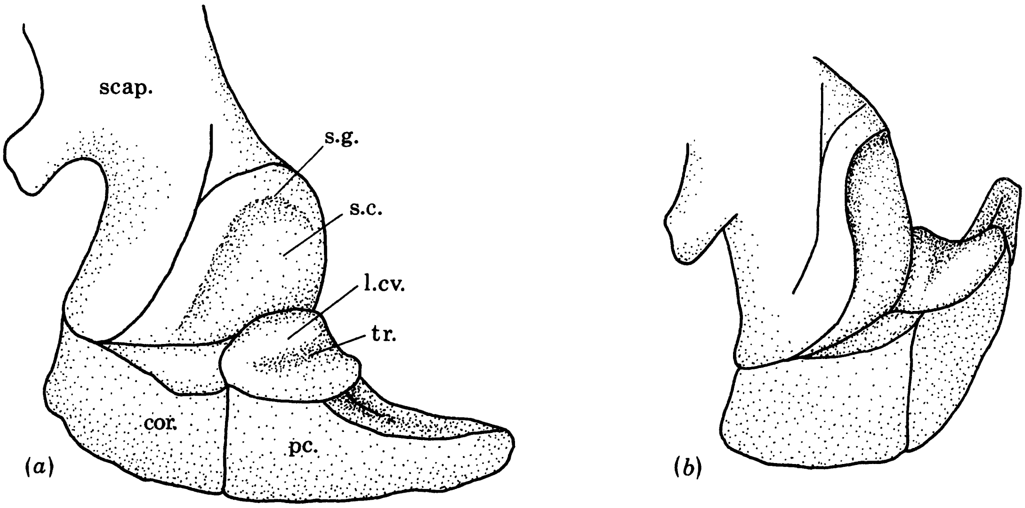


FIGURE 24. Part of the left side of the pectoral girdle to show the glenoid: (*a*) lateral; (*b*) antero-lateral. (Approximately three-quarters natural size.)

(iii) *The lower limb*

The radius and ulna are well preserved, although the radius has suffered some distortion. They have lost some surface detail and the proximal end of each is slightly damaged. However, they still articulate quite well with the relevant surfaces of the humerus.

The ulna (figure 25) is a rod of bone more than half the length of the humerus, flattened antero-posteriorly. The distal end is slightly expanded, particularly on the medial side of the anterior surface. This expanded area bears an oval rugosity, marked by deep striations and ridges, on the anterior surface (figure 25*b*: o.r.). The proximal end of the bone is more expanded. On its antero-medially facing surface there is a triangular facet for reception of part of the head of the radius (figure 25*a*: ru.f.). The proximal end is expanded dorsally to form the olecranon process (figure 25*a*, *b*: o.p.).

The radius (figure 26) is a more slender bone, smaller than the ulna. The ends of the radius appear more markedly expanded because of the slender shaft. The proximal end is expanded mainly in the postero-lateral direction as a somewhat flattened plate, with a rugose surface (figure 26*b*: r.p.). Part of this contacts the facet on the proximal end of the ulna. The ulna and the radius have been described as forming one continuous, proximal surface for articulation with the humerus (Watson 1960). However, in the present specimen, if the proximal ends of radius and ulna are made to touch over any considerable length, then not only does the distal end of the radius not reach the same level as that of the ulna, but also the distal ends lie at a most uncharacteristic angle to each other. It is probably more reasonable to allow only a small degree of contact of the bones, although their exact configuration, especially of the distal ends, depends on the structure of the carpus, which is not known here. Separation of ulnar and radial articulations is not unknown in dicynodonts: Cox (1972) describes it in *Kawingasaurus*, although here it is correlated with a special mode of locomotion.

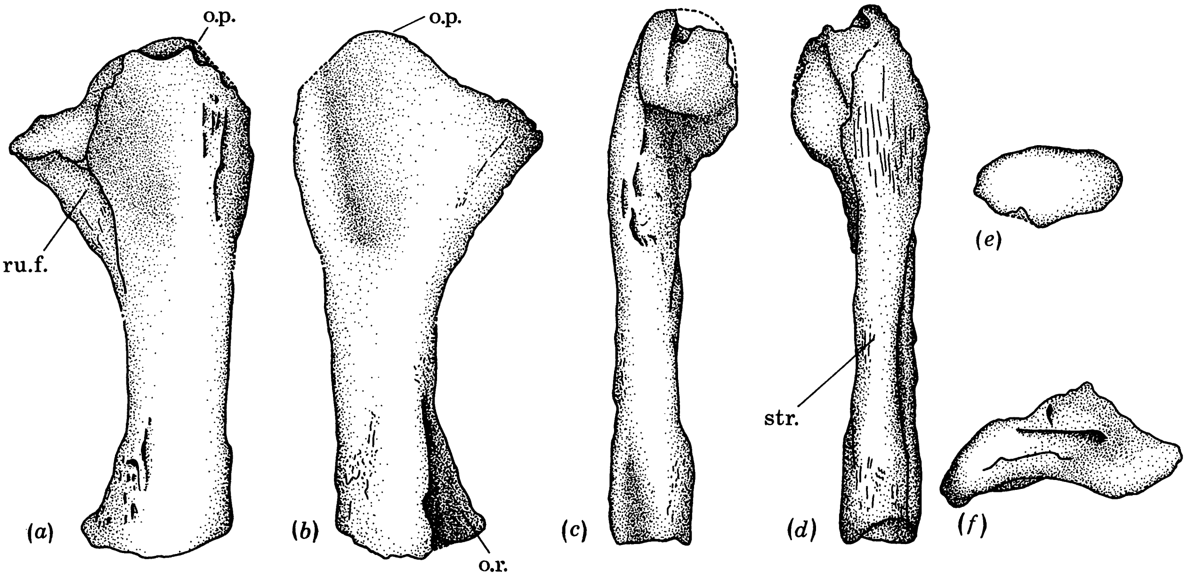


FIGURE 25. The left ulna (three-quarters natural size): (*a*) lateral; (*b*) medial; (*c*) anterior; (*d*) posterior; (*e*) distal; (*f*) proximal.

The trochlea fits comfortably into the articulatory facet on the ulna when the ulna is at 90° to the humerus. On extension the trochlea rolls in the surface of the ulnar facet, and the two surfaces make contact over almost 90° of extension from the vertical. Because of the flattened nature of both trochlea and ulna articulatory facets, a small amount (about 30°) of antero-posterior movement of the ulna relative to the humerus is possible.

The proximal facet of the radius is almost flat. It is pear-shaped, being drawn postero-medially into a sharp ridge down the shaft of the bone (figure 26*e*). It is this ridge that contacts the ulna. There is a good degree of flexibility in movement of the capitellum on the radial facet. The degree of freedom at this joint would allow the flexibility required when the antebrachium moved relative to the humerus during the stride.

The manus of the present specimen of *Dicynodon trigonocephalus* is poorly preserved. Two digits, with three phalanges each, three metacarpals and fragmentary films of bone representing another one or two digits were all found in association with the left radius and ulna. A further two phalanges (one terminal) were found in the loose material gathered from the excavation site of the fossil.

The terminal phalanx is claw-shaped, but does not curve sharply downwards. The claw is rounded-off anteriorly, and thickened posteriorly to form the articulation for the next phalanx.

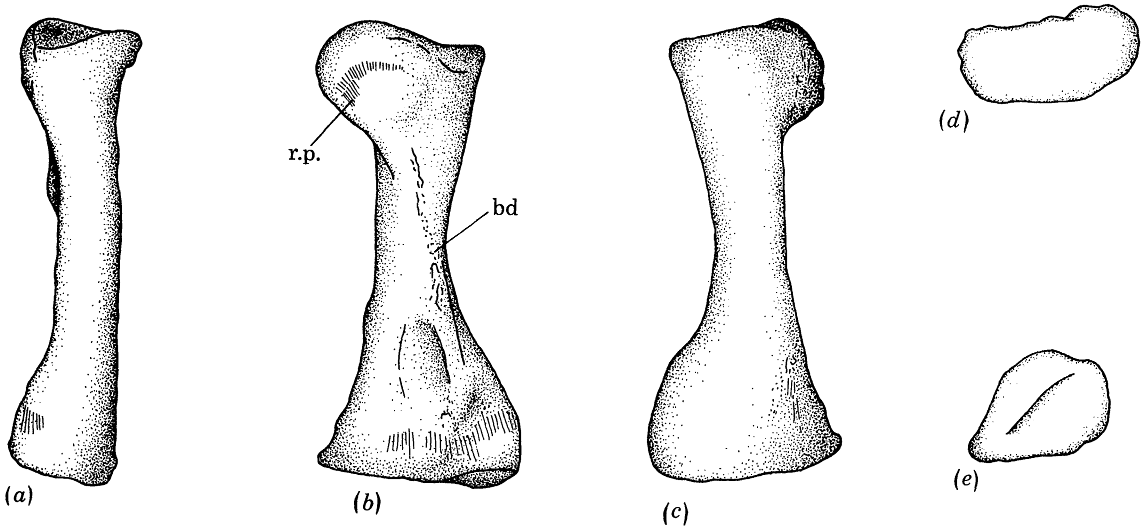
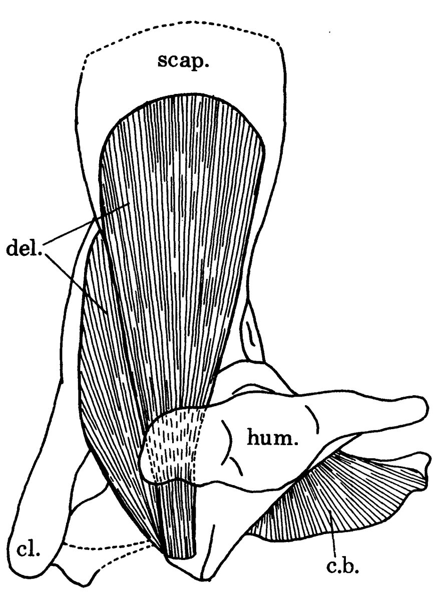


FIGURE 26. The left radius (three-quarters natural size): (*a*) anterior; (*b*) medial; (*c*) lateral; (*d*) distal; (*e*) proximal.



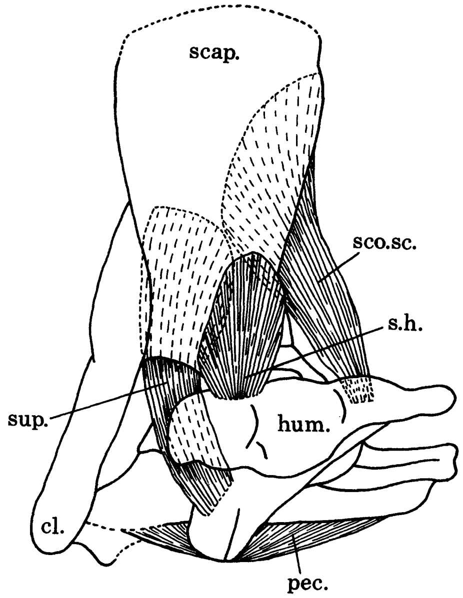


FIGURE 27. Diagram to show the attachments of principle muscles of the pectoral girdle. (Approximately half natural size.)

FIGURE 28. Diagram to show the attachments of the principal muscles of the pectoral girdle. (Approximately half natural size.)

This articulation is almost bicondylic and permits flexion and extension but presumably little else. The digits preserved are similar in size and proportions and so they are probably two out of digits 2, 3 and 4.

Unfortunately, because the carpus is missing, little can be said about the possibility of different movements of the hand. Certainly the digits could flex, probably quite strongly. The claws bear on their ventral surfaces definite raised mounds which are surrounded by radiating striations. These may be the attachment for ligaments concerned with flexing the digits. The hand was probably as wide as it was long, and rather flat. The long, flattened claws may represent a compromise between the need to have as strong and extensive a platform as possible to support the heavy head and thorax, and the need for a digging or scraping tool. Watson (1960) noted that the forefoot is longer than the hindfoot in the species he studied. He concluded that this is because the hindfoot carries the comparatively more slender part of the body and negligible tail.

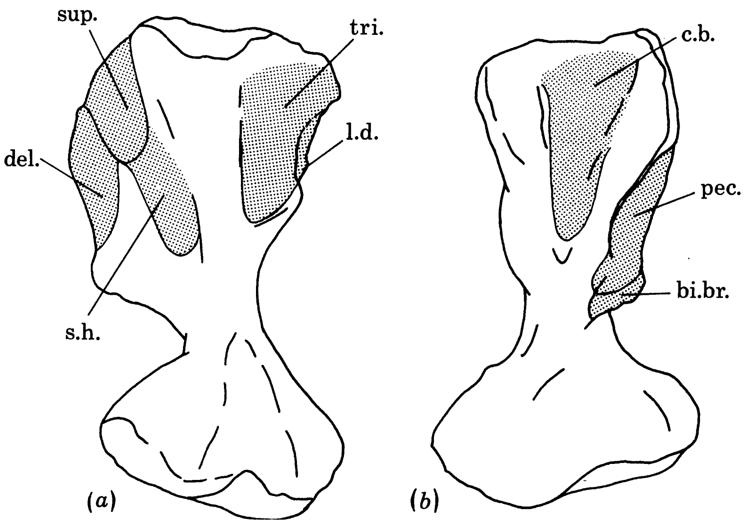


Figure 29. Diagram to show the principle muscle insertions on the left humerus (natural size *ca.* 0.45): (*a*) dorsal; (*b*) ventral.

(iv) *Musculature*

As indicated already the main movements of the humerus are protraction and retraction. Long axis rotation is rather restricted because either the delto-pectoral crest or the postero-medial corner of the head of the humerus collides with the anterior or posterior glenoid surfaces, respectively. However, some of the muscles to be described are in good positions to cause long axis rotation. Reconstructions of the main pectoral muscles are shown in the figures 27, 28, 29. In reconstructing the muscle origins and insertions reference has been made to Romer (1922) in order to establish the presumed primitive condition (in pelycosaurs), and also to compare the dicynodont musculature reconstructed in the present work to other therapsids, and to mammals.

The pectoralis presumably inserts on the ventral surface of the distal part of the delto-pectoral crest (figure 29*b*: pec.). Its origin is probably on the ventral surfaces of the interclavicle and sternum (figure 28: pec.). The sternum bears a fossa on its ventral surface, either side of a midline ridge (figure 22*d*: fo.) which might have housed part of the origin. The muscle runs medially. It will produce some protraction when the humerus is in a retracted position, but its value as an adductor is probably greater. This is also a muscle that could cause some long axis rotation in the clockwise direction on the left side. The supracoracoideus is one of the main protractor muscles. The insertion of the muscle, presumably on the dorsal surface of the delto-pectoral crest, is not marked. The muscle probably ran forward and upward to pass medial to the acromion process and insert on the medial surface of the scapula (figure 28: sup.). The lower edge of the acromion is rounded and smooth, and the process is turned out strongly laterally to allow the muscle to pass. On the medial surface of the scapula there is a fossa dorsal to the acromion process, bounded antero-dorsally by a band of fine, regular striations and pits (figure 20*d*: d.f.). This area may, then, represent the supracoracoideus origin as Watson (1917) suggested. There is no indication of part of the supracoracoideus retaining an insertion on the lateral surface of scapula and procoracoid. The other main retractor is the deltoideus muscle mass. This probably inserts on the dorsal proximal surface of the delto-pectoral crest, and has origins on the scapula and clavicle (figures 29*a*, 27: del.). The scapula origin probably attaches to most of the lateral scapula surface, which is a smooth, shallow fossa. Its action would be humeral protraction with elevation. The clavicular head of the deltoid causes protraction with less of this elevation.

The scapular deltoid would seem to produce a motion very similar to that of the supracoracoideus, although neither muscle is in an ideal position to produce protraction. The supracoracoideus is inserted close to the head of the humerus, and has its origin and insertion almost vertically in line. Its moment arm is therefore very small. The scapula deltoid is in a more advantageous position, being inserted more anterior to the humerus head. Protraction must have been a fairly weak action, most of the muscles responsible for it having a considerable inward or upward pull, rather than forward. The supracoracoideus may have been able to produce long axis rotation, clockwise on the left hand side, which would produce a forward movement of the antebrachium, if one assumes that this is not anchored to the ground.

The main retractor is the latissimus dorsi. Its probable origin from the dorsal fascia is obviously not marked, but there is a strong tuberosity on the posterior edge of the humerus for its insertion (figure 29*a*: l.d.). The strength of its pull cannot be judged accurately, without knowing its origin, but it must be kept in mind that the glenoid has no posterior wall to prevent dislocation of the humerus. It is unlikely that other muscles could prevent dislocation either (see below), and so the pull of the latissimus dorsi was probably not particularly strong.

The other possible retractors are the subcoraco-scapularis and subscapularis muscles. These muscles probably insert on the postero-medial corner of the humerus, on its dorsal and ventral surfaces, proximal to the latissimus dorsi insertion. They most likely originate from the medial and posterior surfaces of the scapula, above the triceps insertion (figure 28: sco.sc.). The posterior scapula surface in this area is smooth, fairly wide and rounded. It leads round on to the medial side without obstacle. The area of origin of the muscles probably extends a good way dorsally, keeping posterior to the origin of the supracoracoideus. The subcoraco-scapularis and subscapularis might cause some retraction, but their origin is far too anterior for this to be substantial. However, they are in a very good position to produce long axis rotation of the humerus, anticlockwise on the left hand side, which would force the antebrachium back, or if this were anchored, would move the body forwards.

In contrast to the scarcity of muscles that can cause protraction and retraction, strong adductors and elevators are plentiful. The pectoralis and scapular deltoid have been mentioned already. In addition the scapulo-humeralis anterior must have had an adducting role. Its origin, from the fossa anterior to the triceps tubercle on the posterior edge of the scapula, and its insertion, in the fossa on the anterior dorsal proximal surface of the humerus, are almost above one another (figures 29*a*: s.h.). It could produce hardly any retraction, protraction or long axis rotation, therefore, but would have been an efficient elevator.

The coraco-brachialis would have been a powerful ventral adductor. Its insertion probably spreads over the large fossa on the ventral proximal surface of the humerus (figure 29*b*: c.b.).

Its origin most likely was on the posterior part of the coracoid, presumably occupying most of the ventro-lateral surface of this bone, and possibly extending onto the ventro-lateral surface of the procoracoid (figure 27: c.b.).

The action of the anterior serratus superficialis as a glenoid rotator has already been noted. Its insertion was probably along the posterior medial margin of the scapula. The left scapula, although damaged, suggests a ridge and striated site in this area. The origin of the serratus anterior superficialis was from the thickened anterior dorsal ribs (9 and 10), as explained in the next section.

The other main muscles of which there is evidence in the *Dicynodon trigonocephalus* specimen are the biceps and triceps. The biceps inserts on the radius and ulna, probably over a considerable length of the head and shaft of these bones. Possible indications of the insertions are the rugose strip on the postero-medial edge of the ulna (figure 25*d*: str.), and the sloping band of striations seen on the postero-medial and posterior surfaces of the radius (figure 26: bd.). The insertions seem to take up a large proportion of the length of these bones, but this is necessary because the bones are fairly short. The origin of the biceps (and the brachialis inferior which merges into it) are from the ventro-lateral surface of the delto-pectoral crest and from the ventro-lateral surface of the coracoid: possibly the marked fossa of the posterior margin (figure 23*e*: fo.). The biceps is therefore an extensive and powerful flexor.

The triceps probably has two distinct origins. The lateral scapular head attached to the pronounced triceps tubercle already noted (figure 20*c*: rug.). The lateral humeral head probably originates from the shallow fossa anterior to the latissimus dorsi tubercle on the posterior margin of the humerus (figure 29*a*: tri.). The medial humeral origin is indistinct and cannot be differentiated from that of the lateral humeral head. The medial coracoid head also was probably not present. In primitive reptiles the origin of this is a roughened area on the posterior end of the coracoid, but a muscle in this position in the present specimen would need to rise up over the posterior edge of the humerus to reach the ulna. The insertion of the triceps is on the olecranon process of the ulna, which is heavily striated and ridged. The triceps would therefore extend the forearm, perhaps forcing it a little anteriorly also, and, as explained previously, the humero-ulnar articulation would permit this. The obvious power of this muscle, apparent from its marked insertion on the scapula, indicates that forearm extension probably played a significant part in the stride.

(v) *Discussion*

The musculature associated with the pectoral girdle and forelimb is extremely powerful, yet does not seem to be adapted to use much of this power to produce a powerful locomotory thrust. The latissimus dorsi seems to be the only reasonably large, well placed muscle to cause retraction, but it may also tend to pull the humerus out of the glenoid, as explained earlier, and its actual use in retraction might therefore be limited. Indeed, the use of the triceps in producing locomotory thrust by extending the forearm may have been more significant. However, the muscles providing adduction and elevation are massively developed. This would indicate that the job of the forelimb was mainly to produce a stable, strong base for the anterior body region. It will be seen later that the forelimbs have a greater track width than have the hindlimbs, presumably giving greater stability, as long as sufficient postural musculature is available, which appears to be so. The origin of the supracoracoideus is interesting in this respect. It has spread over the medial surface of the scapula, as do the mammalian spinatus muscles, but its principal action is elevation, rather than protraction. The supracoracoideus could also cause long axis rotation.

Coupled with this great stability is the short antebrachium, and the presumed plantigrade foot. A wide, flat foot will obviously aid stability, but the shortness of the antebrachium is more difficult to explain. Since the humerus is horizontal, adding nothing to the height of the limb, the antebrachium must be long enough to keep the thorax off the ground. Judging from the limited information available on rib size and orientation, it could do this, but in normal circumstances the front of the body would only be a few inches off the ground. Bakker (1971) correlates a small antebrachium to humerus ratio with a low activity temperature. A large limb length to body mass ratio is associated with basking behaviour in modern lizards, since these need to be able to escape from their basking places, which would be exposed. A longer limb with a delto-pectoral crest high up on the limb permits a rapid stroke, but reduces the thrust that can be applied to the ground to move the body. Conversely, the short limbs are taken to represent avoidance of open spaces by cryptic behaviour or use of undergrowth and dense vegetation as a habitat. For ectothemic animals these niches would represent adaptations to activity at lower temperatures than, say, a lizard that gains body heat by basking.

Bakker's work was applied to lizards, but two general points might apply to *D. trigonocephalus*. One is that the short front limbs do indicate that the front stride was not rapid, but was presumably well controlled and extremely stable. The length of the stride may not be as short as it seems at first consideration: although the protraction–retraction arc is fairly short, various mechanisms are employed to lengthen this, namely long axis rotation, glenoid rotation and extension of the antebrachium on the humerus.

The second point concerns the habits and behaviour of *D. trigonocephalus*, whether it was indeed cryptic or secretive, and so had no need of rapid escape reactions, or whether the slow powerful gait was an adaptation merely towards transporting a massive body. This will be discussed further in the concluding section.

As will be seen when the hindlimb is discussed, the morphology and functional anatomy of the hind and forelimbs is very different, and it is clear that the two regions could not have carried out similar roles in the locomotory cycle at all.

Hindlimb and pelvic girdle

(i) *General*

The left side of the pelvic girdle is represented by a well preserved ilium and an almost complete, though weathered pubio-ischiadic plate in three pieces. The right side consists of the acetabular portion and anterior edge of the ilium and a pubo-ischiadic plate, well preserved except for the acetabular surface. Both left and right femora are preserved but there is no trace of tibia, fibula or foot bones.

By articulating the femur in the acetabulum it becomes apparent that a distinct head is necessary to provide anything more than the most restricted movements. A head was therefore reconstructed, facing mostly antero-dorsal, as the rugose area on the proximal anterior corner of the bone would suggest..

(ii) *Osteology*

It is assumed that at the level of the sacrum the vertebral column is sloping postero-ventrally at a slight angle (no more than 10°) to the horizontal. There is no firm evidence for the curva-

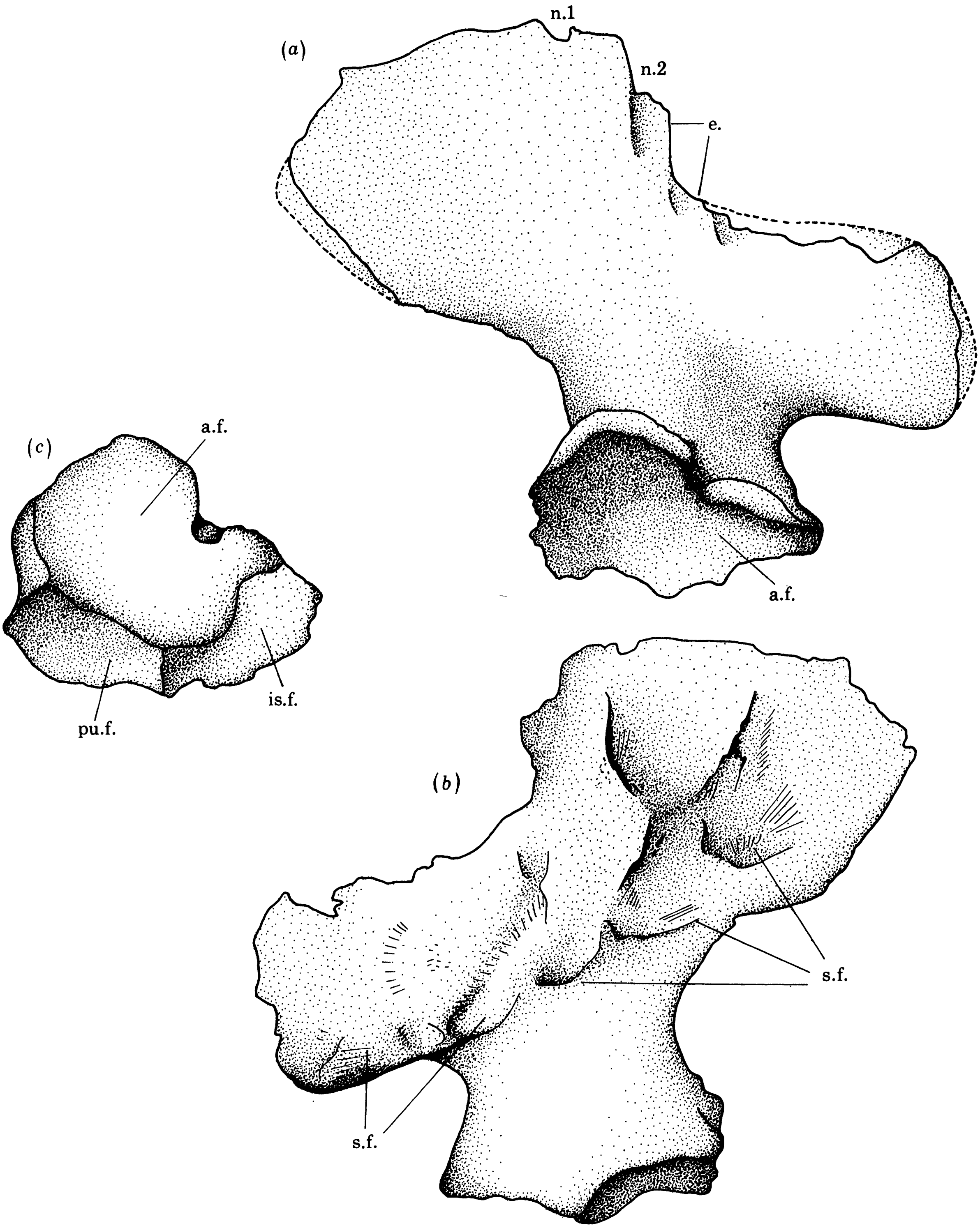


FIGURE 30. The left ilium (natural size): (*a*) dorso-lateral; (*b*) ventro-medial; (*c*) the acetabulum. The broken line represents reconstructed edges.

ture of the spine as reconstructed in figure 44. Orientation of neural spines, transverse processes or zygapophyses gives no clue to the relative position of the vertebrae, and therefore the situation in modern primitive mammals has been used as a model. The vertebrae fit comfortably into such a reconstruction.

The ilium of *D. trigonocephalus* (figure 30) is composed of a flat, dorso-medially orientated plate of bone, which gradually thickens, then constricts sharply to give rise to the process of bone that bears the acetabular facet laterally (figure 30*a*: a.f.) and the facets for the pubis and ischium antero-ventrally and postero-ventrally respectively (figure 30*c*: pu.f., is.f.). The medial surface of the blade has well marked facets for the ends of the five sacral ribs (figure 30*b*: s.f.). The line of the facets curves along the ventral limit of the blade where it is thickest, rather than being in a straight line. The facets for the first and second ribs are the largest and most prominent. The third and fourth facets are similar in area, but the fifth is more elongated and less distinct than the other facets. All facet surfaces bear marked striations and pitting. The marked sculpturing of the rib facets probably indicates extensive strengthening of the sacro-iliac joint by ligaments, since none of the sacral ribs are fused to the ilium. Both Cox (1959) and Cruickshank (1967) have mentioned, without further discussion, the possibility that the ilium and the pubo-ischiadic plate might move relative to one another in *Kingoria* and *Tetragonias* respectively. Certain aspects of the pelvic girdle of *D. trigonocephalus* do indicate a loss of rigidity due to loss of bony connections, for example lack of fusion between sacral ribs and ilium, lack of fusion between all the sacral vertebrae, and lack of fusion between pubis, ischium and ilium. *D. trigonocephalus* does not appear to be a juvenile animal, so presumably strengthening of the pelvic girdle attachment was by means of ligaments. If, then, some of these ligaments were elastic, relative ilium–pubo-ischiadic plate movement would be possible. The possibility of such movements, whether active or passive, may reflect the need for shock absorption, or merely the lack of necessity for a particularly strong girdle–sacrum connection.

Because the ilium has such exceptionally well preserved facets for sacral ribs the pelvic girdle can be articulated with the sacrum with a good degree of certainty of the exact orientation. So positioned, and allowing for the spinal curvature, the iliac blade slopes dorso-medially from the acetabulum. The anterior and posterior ventral edges of the blade are aligned along the horizontal. The posterior dorsal edge of the acetabulum is almost horizontal. The anterior edge of the iliac blade is level with the anterior face of the first sacral vertebra. Because of the long sacrum the acetabulum is not postsacral as in some dicynodonts described, such as *Dicynodon halli* (Watson 1960), but lies lateral to the fourth and fifth sacral vertebrae, and just ventral to their ventral surfaces.

The pubo-ischiadic plate (figure 31) is reconstructed as a triangle, aligned with long sides vertically and postero-dorsally. When in articulation with the ilium, it faces laterally and ventrally. Much of the plate is posterior to the acetabulum. Anteriorly and ventrally the plate is extremely thin. The anterior edge (formed by the pubis) bears a marked pubic tubercle (figure 31*a*: pu.t.), which has pronounced striations and ridges running towards its antero-lateral termination.

Most of the ventral edges of the plates from both sides are present and these are directed medially at a considerable angle when the ilium, pubo-ischiadic plate and sacrum are correctly articulated. It is therefore possible that a pubo-ischiadic symphysis existed, but it was not a strong, bony connection. It may have relied on a cartilage connection, which would have allowed some flexibility. Presence of a definite bony symphysis is unusual in dicynodonts:

Cox (1959) remarks that evidence for a bony symphysis is limited; Watson (1960) thinks that the asymphysial condition may be an adaptation to egg-laying. The pelvis of *D. trigonocephalus* then seems to be a mixture of strength (with the large number of sacral vertebrae, and a pubo-ischiadic symphysis) and flexibility.

The acetabulum articulatory surface as reconstructed is a moderately deep hollow, part of the surface of a sphere excavated in a triangular process of bone formed where the ilium, pubis and ischium meet (figure 30*c*). Antero-ventrally and postero-ventrally it extends into a distinct bony shelf, formed by the articulatory facets of the pubis and ischium. The ilium is not extended on the antero-dorsal or postero-dorsal margins of the acetabulum in such a manner, so the acetabulum is 'open' dorsally. No bony buttresses are present on the acetabulum but the dorsal and posterior angles of the triangle are slightly built up and rounded. When the ilium is placed on the sacral vertebrae, the acetabulum faces almost directly laterally.

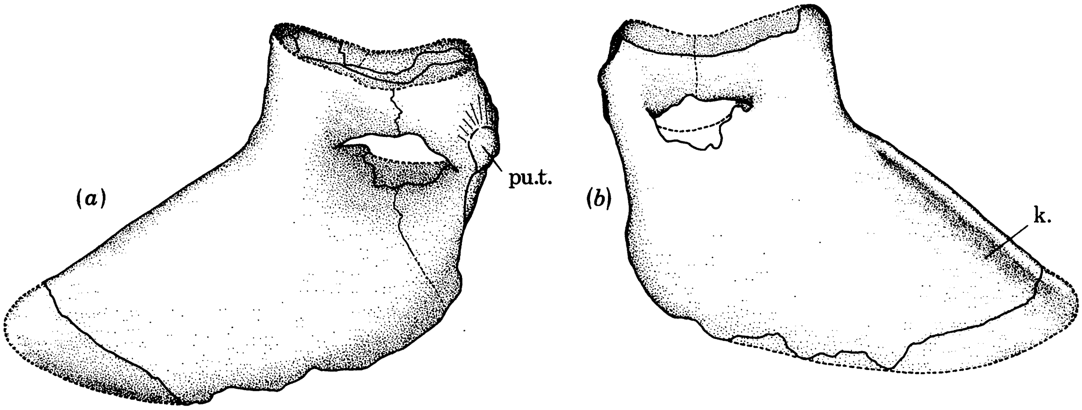


FIGURE 31. The right pubo-ischiadic plate (three-fifths natural size): (*a*) ventro-lateral; (*b*) dorso-medial. The broken line represents the reconstructed edge.

The femur (figure 32) is a dorso-ventrally flattened rod of bone with a distinct shaft between the expanded distal and proximal ends. The articulating head (figure 32*a*, *b*: h.) of the bone is on the anterior margin and encroaches on the dorsal surface. There is no distinct neck. Posterior to the head the bone is expanded along half its length to form the flat plate that bears the trochanter major proximally (figure 32*a*, *d*: tr.m.).

With the head articulating in the acetabulum the femur can be protracted to a position where its long axis is almost parallel to the sagittal plane of the animal. There are no bony constraints on this protraction, although possibly stretching of the muscles would act as some constraint. In the protracted position the long axis of the femur makes an angle of approximately 40° to the vertical (figure 33*a*). From the fully protracted position the femur is pulled upwards and backwards to its maximally retracted position (figure 33*b*), in line with the centre of the acetabulum. The trochanter major prevents any further backward movement. The femur is now in a more 'sprawling' position, making an angle of approximately 75° to the vertical, and the ventral surface of the head is resting on the ischiadic ledge of the acetabulum. From this position the femur can be rotated about its long axis (anticlockwise on the left hand side) through at least 60° until the proximal end just posterior to the head abuts the dorsal thickened angle (figure 33*c*). In this position the tibial condyle would probably face almost directly backwards and only slightly downwards. The orientation of the tibia and fibia is difficult to deduce since not only are these bones missing from the present specimen, but also the posterior

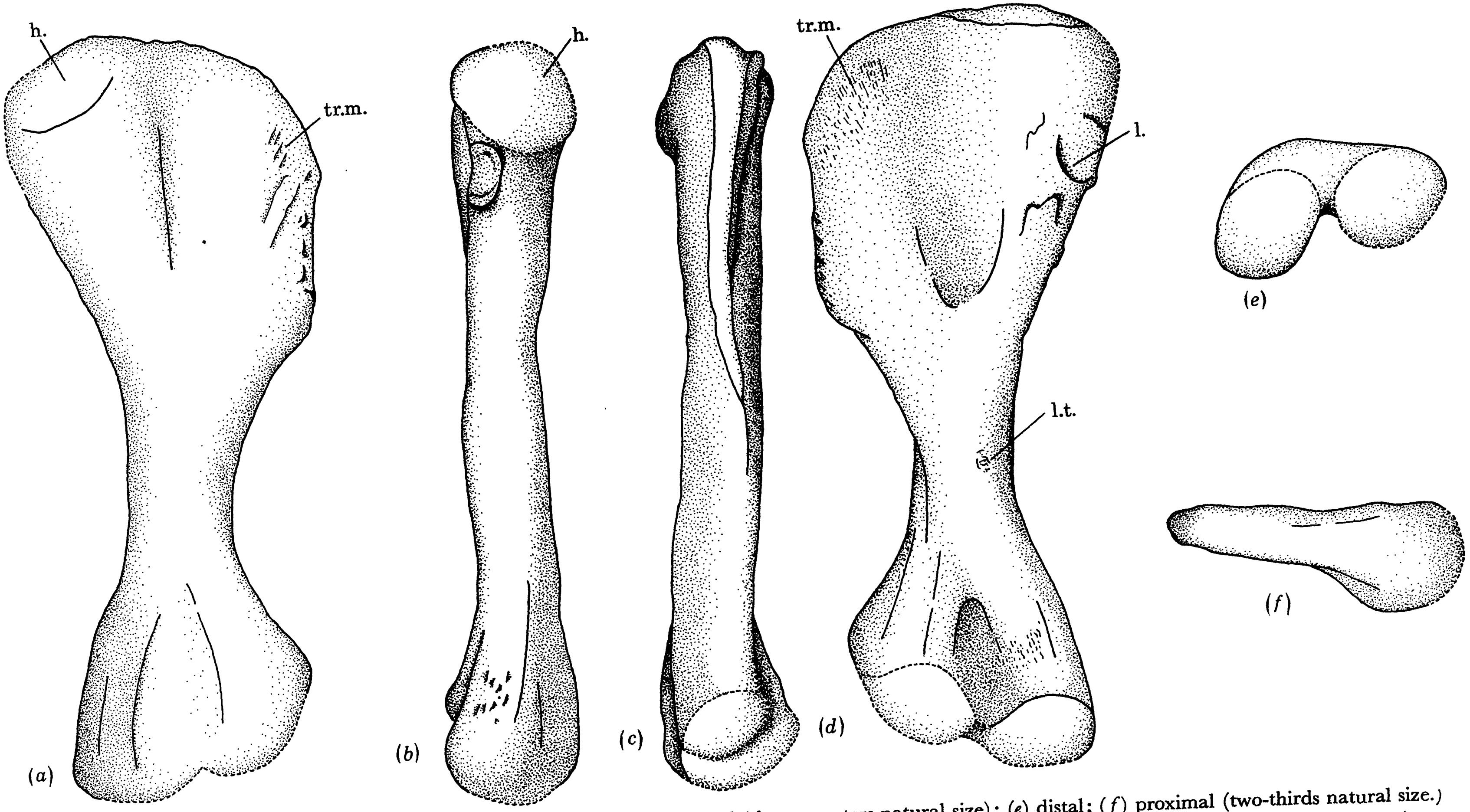


FIGURE 32. The left femur: (*a*) dorsal; (*b*) anterior; (*c*) posterior; (*d*) ventral (three-quarters natural size); (*e*) distal; (*f*) proximal (two-thirds natural size.)

of the two condyles for articulation with the tibia and that for articulation with the fibula are missing from the femur. However, it would seem that if the tibia and fibula did extend while the femur was in the position described above then their only contribution to movement would be to force the femur medially. However, another possibility exists. Once the femur has rotated about its long axis the trochanter major will project postero-dorsally from the acetabulum and the femur may now be retracted further without the trochanter knocking on the posterior rim of the acetabulum (figure 33*d*). The tibial condyles still face backwards and slightly downwards, but, since the femur is now orientated backwardly instead of laterally, when the limb is extended the motion produced has a significant forward component.

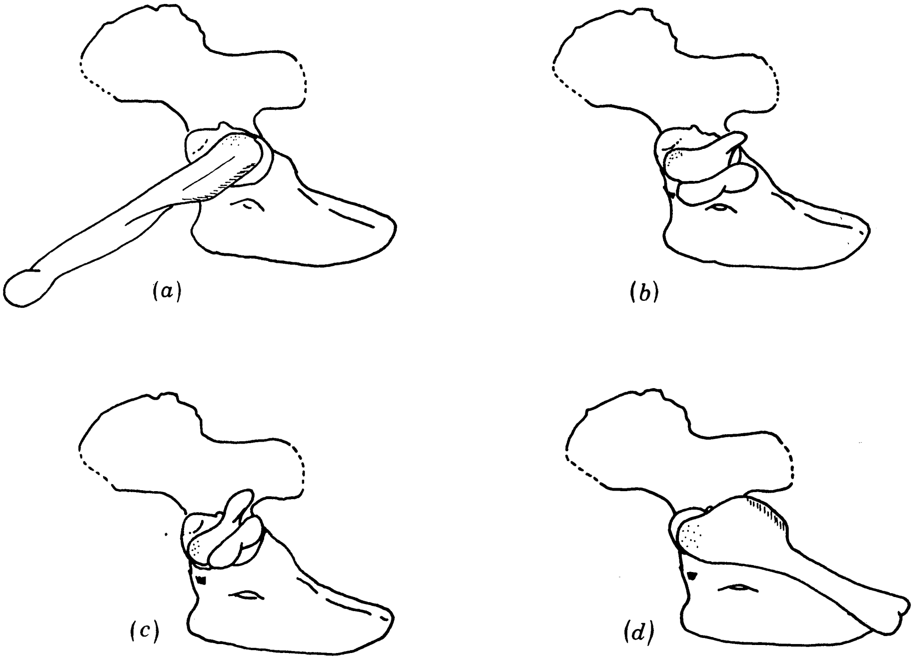


FIGURE 33. Diagram to illustrate different stages in the stride of the hindlimb. Seen from the left. (*a*) Protraction, the femur is in a semierect position; (*b*) retraction, the femur is in a more 'sprawling' position; (*c*) long axis rotation; (*d*) further retraction: the femur is semierect.

Movement of the femur would therefore seem to be a complex process. 'Retraction' from a protracted position involves the following elements: retraction and abduction from a semi-erect position to a more sprawling position; long axis rotation changing the orientation of the tibial condyles and causing the trochanter major to project postero-laterally; further retraction to a final position. A seemingly obvious way to simplify this complex movement would be to retain the semierect position of the femur from initial retraction and thus keep the trochanter major laterally directed to prevent it knocking on the acetabulum. The femur could then be retracted in one simple almost parasagittal movement. However, this means that the tibia and fibula must undergo an improbable amount of flexion to allow the femur to pass through the lowest part of its swing, since the propodials appear to be orientated almost at right angles to the femur, as in a normal sprawling gait. Also it will be shown that the muscle pattern present does not produce such a simple parasagittal swing. Therefore *D. trigonocephalus* appears to show a mosaic of advanced and primitive characters: the femur can assume a semierect position, at least through part of the stride, but the orientation of tibia and fibula has not been altered to allow a simple parasagittal swing, neither are the main retracting muscles sufficiently modified from the primitive condition to produce a parasagittal swing. This notwithstanding, this dicynodont could produce a fairly extensive and powerful stride, as explained below.

(iii) *Musculature*

The postulated origins and insertions of the important pelvic girdle and hindlimb muscles are shown in figures 34 and 35. Although the bones of TSK 14 are well preserved, the positions of some of the muscles are conjectural and much reference has been made to the papers of Romer (1922) and of Gregory & Camp (1918).

From the above description of the motion of the femur, muscles to perform the following actions are necessary:

during retraction,

(1) to keep the foot firmly on the ground,
(2) to pull the femur up and back,
(3) to rotate the femur (anticlockwise on the left hand side),
(4) to pull the femur down and back,
(5) to extend the limb;

during recovery,

(1) to lift the foot,
(2) to flex the limb,
(3) to pull the femur down and forward,
(4) to rotate the femur if this does not occur automatically in (3).

The adductor femoris may perform some part of the work of placing the foot on the ground and keeping it there during retraction. The insertion of the adductors is reconstructed along the antero-ventral edge of the distal part of the femur, where a low tubercle is seen (figure 34*c*: l.t.). The tubercle continues more proximally into a band of irregular striations in the centre of which is a small but marked swelling. These markings are taken to indicate the extensive insertion of the adductor femoris (figure 34*c*: add.). The origin is not marked but is presumably from the ventral margin of the pubo-ischiadic plate. The adductor femoris is therefore an extensive muscle and in a suitable orientation to pull the femur down somewhat. Its far distal insertion ensures that the downward force will act as far as possible through the crus and foot and will reduce bending of the femur which would be induced if the insertion were more proximal. Its anterior insertion would also produce a small amount of long axis rotation (anticlockwise on the left hand side) needed in stage 3. Also, in the initial stages of retraction the adductors would contribute a small retractive force. However, the pubo-ischio-femoralis externus also contributes to keeping the foot on the ground, as described later.

In stage 2 the femur is pulled up and back, pivoting about the head in the acetabulum. The ilio-femoralis muscle is the obvious candidate to cause this movement. However, the muscle has a complex action. Its origin is presumably from much of the lateral surface of the iliac blade. Compared to that of such forms as *Dimetrodon* or *Moschops* (Romer 1922) the anterior margin of the ilium is much expanded. Also, the posterior part of the iliac blade is considerable, having an expanded ventral area. It would therefore be expected that these areas would be important from the point of view of the origin of the ilio-femoralis. The insertion of the ilio-femoralis is on the trochanter major (figure 34*b*, *c*: i.f.). In dicynodonts this area is not marked off from the head by a distinct neck and is continued distally almost halfway down the shaft as an extensive plate. The edge of this plate is deeply striated. Dorsally the plate bears a very concave triangular fossa over much of its area. Cruickshank (1967) suggests that an incipient third trochanter is present in *Tetragonias* (see also Parrington 1961). Some modern perissodactyls and other mammals possess a third trochanter for insertion of a slip of the ilio-femoralis. Gregory (1912) also notes that in graviportal animals the third trochanter and trochanter major are connected by a ridge, as would be the situation in *Tetragonias*. The present specimen of *D. trigonocephalus* shows no sign of a separate third trochanter. However, the deep striations on the elongated trochanter major have been noted, and the ilio-femoralis probably inserted along most of the ventral margin. More anteriorly (considering the femur to be in a sprawling position, half retracted) a low, indistinct ridge probably marks off this insertion from that of the pubo-ischio-femoralis externus. The insertion of the ilio-femoralis may also have extended over the edge of the trochanter to the dorsal surface, since no other muscle insertion can be postulated for the very definite markings there.

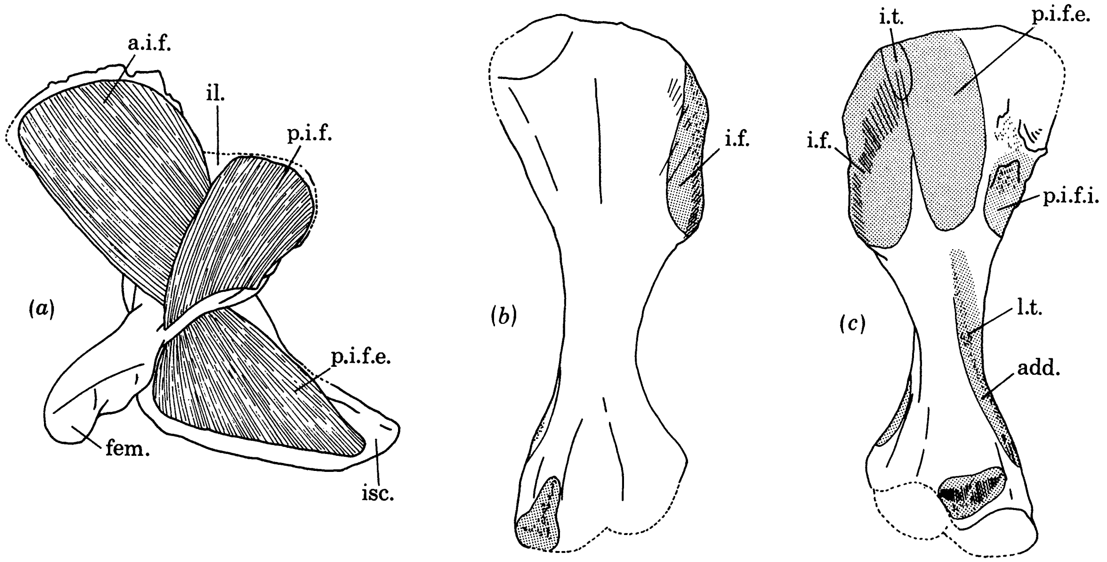


FIGURE 34. (*a*) The attachments of principal muscles of the pelvic girdle. (Approximately one-third natural size). (*b*), (*c*) The insertions of muscles on the left femur: (*b*) dorsal; (*c*) ventral. (Natural size × *ca.* 0.53.)

It has been suggested above that the action of the ilio-femoralis was complex. In order to produce the initial backward and upward pull necessary in stage 2 of retraction, a section of the muscle from the proximal and distal parts of the trochanter, both dorsal and ventral surfaces, is necessary. This would insert on the backwardly produced area of the iliac blade and would produce upward and backward movement, with a little long axis rotation (figure 34*a*: p.i.f.). Fibres of the muscle must run from the proximal and distal ventral surfaces of the trochanter to the anterior extension of the ilium (figure 34*a*: a.i.f.). These can produce no retraction of the femur, since they run anterior to the centre of the acetabulum. They will, however, produce long axis rotation (anticlockwise on the left hand side). In stage 2 of retraction, contraction of the anterior fibres would oppose the action of the posterior fibres and therefore the two parts of the muscle must have had independent and sequential actions. There is a small area of the iliac blade where neither part of the ilio-femoralis can attach with very much advantage, and this is interesting in the context of reconstructing the shape of the iliac blade. At first sight it seems that a complete hemispherical plate is the most likely reconstruction. However, the notch, n.1, the edge, e., and possibly the notch n.2 (figure 30*a*) on closer examination are seen to be undamaged edges. This leads to two possibilities: either that the dorsal margin of the ilium is notched as Watson (1912) describes in *Lystrosaurus* or, if n.2 is an artefact, that the ilium blade is divided into two lobes, the edge, e., constituting part of the posterior border of one of them. Possibly, then, the anterior and posterior margins of the blade are being built up whereas the less advantageous central region is being reduced. As this happens the ilio-femoralis tends to become differentiated into a posterior component causing retraction and a little long axis rotation, and the anterior component mainly responsible for long axis rotation.

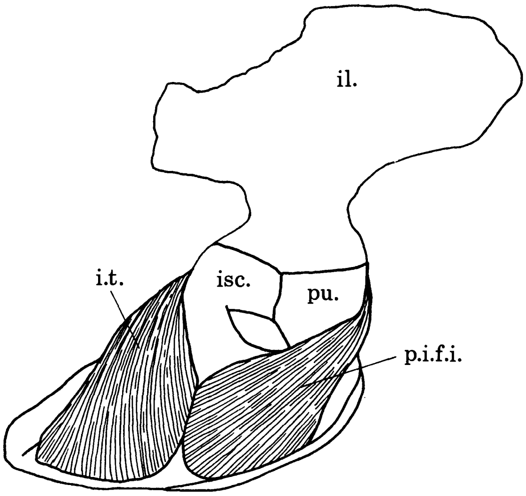


FIGURE 35. The attachments of principal muscles to the medial side of the pelvic girdle. (Approximately one-half natural size.)

Having rotated, the femur is brought down and back to its fully retracted position, stage 4. The ischio-trochantericus and possibly pubo-ischio-femoralis externus are involved here. The ischio-trochantericus is probably the more important muscle. The insertion on the femur is normally tendinous, according to Romer (1922). A possible place for this insertion is the particularly rugose area on the ventral surface of the trochanter major between the insertions of the proximal component of the ilio-femoralis and the pubo-ischio-femoralis externus (figure 34*c*: i.t.). From its insertion the muscle passes backwards and downwards over the smooth and broad posterior dorsal margin of the ischium, to attach to its internal surface (figure 35: i.t.). The posterior edge of the ischium is thickened throughout its length. About one-third of the way down towards the ventral termination, the edge turns medially, forming a robust keel (figure 31*b*: k.). This bears a resemblance in position and orientation to the triangular flange of the ischium described by Pearson in *Kannemeyeria* (1924) in connection with the ischio-trochantericus. The flange or keel seems of variable occurrence in the dicynodonts: two other specimens examined, TSK̦ 37 and *Dicynodon sollasi* (number FX 1/1, Geological collections, Oxford University Museum), although having substantial thickening on the postero-dorsal edge of the ischium, have no medially directed flange or keel.

The keel in *D. trigonocephalus* might have one or more of the following uses: it could strengthen the ischiadic plate against the pull of the ischio-trochantericus, which would be an extensive muscle; or it might serve as a further area of attachment for this muscle, as Pearson indicated in *Kannemeyeria*. However, the keel in *D. trigonocephalus* has only a small medial extent, unlike the triangular flange in *Kannemeyeria* and that of *Tetragonias* (Cruickshank 1967). Unfortunately the medial face of the ischium gives no clue to its muscle origins. Whatever the function of the ischiadic keel its association with the origin of the ischio-trocantericus seems to indicate that this was an extensive muscle and, in fact, played an important role in retracting the femur.

The pubo-ischio-femoralis externus, however, appears to be in a disadvantageous position for most phases of the femur's movement. Its origin on the pubo-ischiadic plate is reduced since the plate is rather short antero-posteriorly (figure 34*a*: p.i.f.e.). Its most likely insertion is into the shallow fossa between the head of the femur and the ilio-femoralis insertion (figure 34*c*: p.i.f.e.). So orientated it would induce a downward and backward force on the femur during initial retraction, changing to an adducting force in the half-retracted position. It will tend to oppose long axis rotation to a small degree, possibly preventing over-rotation and stabilizing the joint. If some of its fibres originate from the postero-ventral extremity of the ischium then a small amount of down and backwards pull will be exerted on the femur during stage 4. Generally, however, the usefulness of this muscle as a locomotory muscle has diminished and its importance is more with posture and stabilization of the joint. In this its role is different from that of the adductor femoris since it is acting much nearer the head of the femur, with a considerable downward component serving to keep the head braced against the ventral shelf of the acetabulum, whereas the line of action of the adductor femoris is more directly laterally, keeping the head braced against the middle of the acetabulum. It is presumably because of the action of these two muscles that no dorsal buttressing of the acetabulum is necessary.

The recovery stroke is effected mainly by the pubo-ischio-femoralis internus. This probably inserts on the wide, round swelling on the anterior margin of the ventral surface of the femur (figure 34*c*: p.i.f.i.). Proximally and on its anterior edge this swelling bears a transverse curved ledge (figure 32*d*: l.) which forms the distal boundary of a circular fossa. The muscle passes round the smooth anterior edge of the pubis to its origin on the medial surface of the pubo-ischiadic plate (figure 35: p.i.f.i.). Relaxation of this muscle while the ilio-femoralis is still contracting will cause the femur to be lifted and raise the foot from the ground. The pubo-ischio-femoralis internus will then pull the femur down and forward. Contraction of the ischio-trochantericus will help to control the possible tendency of the pubo-ischio-femoralis internus to cause rotation of the femur. The femur therefore ends its protractive stroke in the semi-erect position.

As tibia and fibula are not present in TSK 14, and the distal ends of both femora are damaged, it is impossible to draw any firm conclusions regarding flexion and extension of the hindlimb. However, a distinct site of origin of the gastrocnemius muscle is present between the internal and external condyle. Also, the attachment of the medial ligament to the tibia is well marked as a rugose band of pitting and striations on the antero-dorsal surface of the distal half of the bone. On the posterior surface of the external condyle a rugosity is present, possibly marking the origin of either a peronaeus longus or extensor communis digitorum. Presumably, then, there were no unusual features in the actions of flexion and extension of the forelimb, although the amount of each movement possible depends on the configuration of the femoral-crus articulations which are not available for study. However, the tibia of another well preserved specimen, TSK 37 has been used to estimate the amount of movement possible, to evaluate the stride length.

No role has been postulated for the caudi-femoralis in limb movement. No definite evidence for either its insertion or origin is present, unless a very small, low boss on the ventral surface of the shaft of the femur marks the insertion (figure 32*d*: l.t.). However, as already noted, this boss is continuous with a line of rugosity postulated as the adductor insertion and is probably associated with these muscles. Similarly, the anterior caudal vertebrae are reduced in size and possess neither fused ribs nor stout transverse processes where a caudi-femoralis might originate. The muscle must therefore have been very small, its role in locomotion taken over by the ilio-femoralis.

(iv) *Discussion*

The length of the stride that the hindlimb could have attained can be broken into two: retraction (including the long axis rotation of the femur) and extension between the femur and crus. During the complex retraction phase outlined above the distal end of the femur moves backwards a distance of approximately 19.0 cm. If the crus is then extended on the hindlimb, possibly 50 % of the movement involved will be in a backward direction, the rest ventro-lateral. This could contribute another 7.5 cm of forwards movement (a conservative estimate). These figures are arrived at by articulating the specimens and directly measuring the extent of the movements produced, not by calculation.

Total stride length is therefore approximately 26.5 cm. This is equivalent to 32 % of the presacral length of the specimen. This seems a reasonable stride. Total width of the trackway is estimated at 52 cm, at the level of the shoulder girdle, and 42 cm at the level of the pelvic girdle. (Width was measured at the distal end of the femur and humerus, with the assumption that the crus and antebrachium are orientated at right angles to the propodials during the widest part of the stride.)

The movement and posture of the hindlimb are therefore advanced over the presumed primitive reptilian condition, that is, with the femur positioned at right angles to the axis of the body. However, the limb appears to be designed to produce a slow, but powerful, stride. Much of the available muscular energy for this is exerted by long axis rotation of the femur by the ilio-femoralis, and the distal expansion of the trochanter major is correlated with the need for attachment of these muscles. Use of long axis rotation for increasing the stride is not unexpected in a therapsid since Jenkins (1970, 1971*a*) and Bakker (1971) both note that in primitive mammal-like reptiles long axis rotation plays an important part in limb movement.

The action of the ischio-trochantericus (obturator internus) in retraction seems to be particularly important and the ischium is elaborated for its origin. The downward component of the ischio-trochantericus makes reduction of a bony dorsal wall to the acetabulum possible. The caudi-femoralis must have been greatly reduced and with it the length and strength of the tail.

Comparing the morphology of the pelvic and pectoral regions, several differences are apparent.

(1) Most of the muscles running from pelvic girdle to femur have their insertions on the ventral surface of the femur. Only the ilio-femoralis is dorsal. In contrast, most of the pectoral muscles insert on the dorsal side of the humerus. Only the coraco-brachialis and pectoralis insert ventrally.

(2) In conjunction with this, it is seen that the acetabulum is open dorsally and antero-dorsally, whereas the glenoid is open ventrally and posteriorly.

These differences must be correlated with the differing forces operating at the joints. The ventral pull of many of the pelvic muscles, which would force the femur against the ventral ledge of the acetabulum, could indicate that during the locomotory cycle considerable force is generated by the hindlimb, tending to dislocate the femur upwards. This is, after all, the direction in which the ilio-femoralis pulls. At the pectoral girdle, there is obviously not such a powerful upward force as no muscle capable of generating it has been noted in the reconstruction. However, possibly there is a tendency to dislocate the humerus in the downward and forward direction, and therefore the powerful dorsal muscles might tend to pull the humerus in against the scapula and coracoid facets of the glenoid to combat this. The tendency to dislocate the humerus in the downward and forward direction could be associated with the movement of the glenoid in an upward and backward direction. Kemp (1980) has proposed that in the primitive cynodont *Procynosuchus* the forelimb generates little or no propulsive force. Instead this is done by the hindlimb, and the forelimb becomes merely the means of supporting the front end of the animal during forward movement. In *Dicynodon trigonocephalus* it can be seen that when the hindlimb generates a locomotory force it is the vertebral column that transmits this force to move the body. The vertebral column is thrust forwards, carrying with it the pectoral girdle, to which it is attached firmly by the axial musculature. Since the lower leg, and therefore indirectly the humerus is firmly fixed, then it is possible that the humerus may tend to lag behind, as the girdle moves forwards, and risk becoming dislocated at the glenoid. The strong elevators and adductors would then be in a position to prevent this possible dislocation, until the foot were removed from the ground to be moved forward. This would allow the forelimb to be kept on the ground as long as possible during the locomotory cycle, again presumably for increased stability.

(3) The head of the long bone in question and the socket in which it articulates are very different in pectoral and pelvic girdles. The acetabulum approaches a rounded socket, whereas the glenoid is more open and provides a smaller surface in relation to head size than does the acetabulum. Again this is probably correlated with the femur generating large locomotory forces and moving through a comparatively large arc, while the motion of the humerus is more restricted.

(4) The pectoral and pelvic girdles are actually in very different parts of the body. The pectoral region bears the massive thorax and the anterior abdomen posteriorly, and the massive head anteriorly. The girdle is joined to the vertical column at a point where the latter shows considerable flexibility. In contrast to this the pelvic region bears the lower abdomen anteriorly and the short tail posteriorly, both very light in comparison to the head and thorax. The pelvic girdle joins the vertebral column in a region where it is extremely rigid; in fact, the sacral vertebrae are fused. Such differences lend more weight to the suggestion that the forelimb and hindlimb must have performed very different tasks because very different constraints must have been acting on them. For example, it is possible to envisage considerable interference to forelimb movement by the motion of the head in feeding and in sensory behaviour. Indeed, the need for greater mobility and strength in the neck region may have been an important consideration in the evolution of the locomotory performance of the front limb in animals other than dicynodonts.

The axial skeleton

(i) *General*

The axial skeleton of the present specimen of *Dicynodon trigonocephalus* is probably complete from the atlas to the tip of the tail, consisting of 45 vertebrae. On the right side, a series of rib heads in varying states of preservation runs from vertebra 4 to vertebra 24. Various lengths of rib are attached to the heads, the longest being approximately 135 mm and incomplete. On the left side a series of rib heads runs from vertebra 6 to vertebra 26. No ribs from the atlas and axis have been recovered.

No intercentra, apart from that of the atlas vertebra, have been found.

The axial skeleton was excavated in several blocks and within these blocks each vertebra is *in situ*, though not necessarily exactly articulated. When the vertebrae are articulated correctly a considerable gap exists between successive centra, and this gap is maintained by pyramidal, shelf-like outgrowths of the neural arch. Presumably these gaps accommodated cartilaginous intervertebral discs. The anterior and posterior faces of the centra appear themselves to have been completed in cartilage since they have a spongy, unfinished appearance.

The structure of the individual vertebrae is similar to that of vertebrae described by other authors, for example, Watson (1960), Cox (1959) and Cox (1965). No dorsally facing metapophyses are present, however, and the neural spines are distinctly backwardly directed.

In all vertebrae where the bone in question is well preserved, the neural arch is seen to be produced posteriorly beyond the face of the centrum as a pyramid whose apex faces posteriorly (figure 38*a*, *b*: py.). One of the faces of the pyramid is directed ventro-medially and is of unfinished bone, possibly covered in cartilage in life. There are similar, though not so marked, anterior projections of the neural arch. When two vertebrae are in articulation, therefore, their centra cannot meet since the anterior and posterior neural arch projections prevent this. However, even if these were not present, when anterior and posterior zygapophyses are correctly aligned with one another, a considerable gap (3 to 4 mm) would exist between adjacent centra.

Every vertebra shows a clear suture between centrum and neural arch. On the anterior edge of the neural spine the line of junction of the two halves of the neural arch is also visible. Just before the two halves of the neural arch begin to diverge at the level of the posterior origin of the zygapophysis, each edge is drawn up into a prominent but small and extremely smooth boss (figure 39*c*: s.b.). Such bosses occur as far forward as the eighteenth vertebra, although poorer condition of the more anterior vertebrae precludes their identification here. Immediately posterior to the boss is a small but marked fossa (figure 39*c*: fo.). The bosses and fossae become more pronounced towards vertebra 26. When successive vertebrae are in articulation, the posterior zygapophysis of one vertebra just fails to meet the anterior bosses of the next posterior vertebra. However, the anterior zygapophysial bosses do align with, though do not contact, the small bosses on the posterior zygapophyses of the vertebra in front (figure 38*g*). These posterior zygapophysial bosses are found on the postero-dorsal surface of the posterior zygapophysis just either side of the midline. They can be seen from vertebra 21 backwards. The posterior bosses take the form of small, laterally projecting shelves. They differ from the general bone surface of the zygapophysial stem, which is pitted and striated, by being capped by extremely smooth bone. The ledges are incipient in vertebra 21, but project strongly in vertebra 25, and reach their most developed condition in the anterior zygapophyses of vertebra 26. As will be explained later, this region of the vertebral column (the posterior dorsal) is characterized by being rather rigid, cutting down flexibility in both sagittal and transverse planes. This is due mainly to the disposition of the zygapophyses. It is not unlikely, therefore, that to supplement the strength of the column ligamentous and muscular 'ties' are used. The zygapophysial structures described could indicate the sites of attachment of ligaments, perhaps with a degree of elasticity that would tie adjacent vertebrae firmly together, but also allow small accommodating movements.

The lateral surfaces of the vertebral centra are marked by various striations and minute pits, but a single large, oval pit is present on every centrum where the bone surface is not badly damaged, from neck to sacrum (see for example, figure 38*a*: pit). In the neck region the pit is low down on the centrum, posterior to the rib facet and just above the level of its ventral margin. Progressing along the vertebral column posteriorly, the position of the pit gradually becomes more dorsal.

Various antero-posterior trends in vertebral structure are seen along the vertebral column and these reflect the different possibilities of movement between vertebrae in different regions of the column. The trends concern mainly the anterior and posterior zygapophyses, the transverse processes and rib articulations, and the neural spines.

(ii) *The atlas–axis complex*

The atlas and axis vertebrae and/or the occipital musculature of dicynodonts have been discussed in detail by Ewer (1961), Cox (1959), Cluver (1971) and Kemp (1969*b*). It is generally agreed that although the morphology of the atlas–axis complex is still basically reptilian, some rotation of the head was possible. Cluver (1971) follows Ewer (1961) in suggesting that rotation took place between the atlas and axis vertebrae; Kemp suggests that this is actually a non-moving joint, and that rotation takes place between atlas neural arch and atlas centrum.

Ewer (1961) reasoned that rotation occurred because she considered the obliquus capitis magnus to be absent in dicynodonts, being a specialization of modern reptiles. She decided that it could not be present in animal groups on the mammalian line as it would rule out independent atlas–axis movement. Furthermore, Ewer considered that the main rotating muscle, the obliquus capitis inferior, is well developed, judging from its areas of insertion and origin.

Cluver (1971) came to the conclusion that rotation between the atlas and axis occurred because the atlas postzygapophysis and axis prezygapophysis were both reduced and therefore would permit rotation.

Kemp (1969*b*) demonstrated that the morphology of the atlas intercentrum and odontoid articulations would allow rotation in dicynodonts, but that this would lead to occlusion of the neural canal by the atlas neural arches. He suggested that the morphology of the atlas neural arch and odontoid allows movement of the neural arch to correct for this occlusion.

Apart from Kemp's work, much of the other evidence depends on the ability to determine accurately the origins and insertions of the occipital musculature. The atlas–axis complex of *D. trigonocephalus* shows some evidence of these attachments (figure 36). It is very similar to the atlas–axis complex of *Kingoria* (Cox 1959) and *Lystrosaurus* (Kemp 1969*b*). Both atlas neural arches are free of the centrum (figure 36*f*–*i*), but the latter is fused to the axis (figure 36*a*). Therefore rotation could not have occurred at this joint as Cluver suggests for *Lystrosaurus*.

A marked facet on the atlas neural arch for articulation of the proatlas is present, in contrast to Kemp's observations (figure 36*f*: pr.). The proatlases are well preserved, each being a narrow, straight sheet of bone (figure 36*l*, *m*). The ventral edge is thickened to form, halfway along its length, the rounded boss that contacts the proatlas facet lateral to the foramen magnum on the occiput (figure 36*m*: o.f.). On its medial surface the plate bears a clear oval facet which is able to contact the neural arch when the atlas is articulated with the occipital condyle (figure 36*m*: n.f.).

The atlas neural arch also bears a well developed transverse process, a lateral process (Cluver 1971) (figure 36*f*: l.p.) and an anterior process just ventro-medial to the proatlas facet (figure 36*f*: a.p.n.).

The axis is of the same general plan as the succeeding vertebrae, with some exceptions

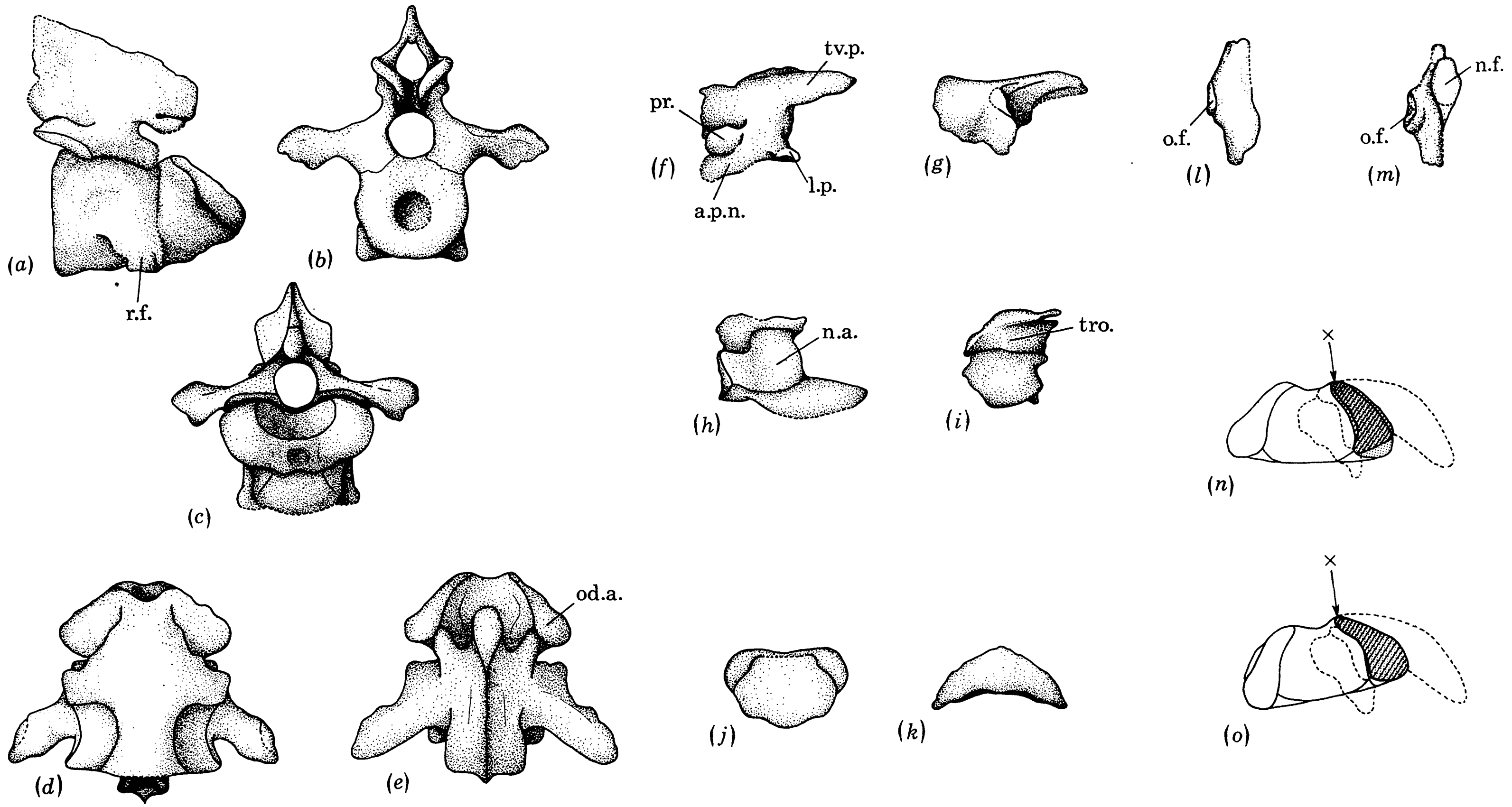


FIGURE 36. The atlas–axis complex. (*a*) The atlas and axis vertebrae in left lateral view; (*b*) the same in posterior view; (*c*) the same in anterior view; (*d*) the same in ventral view; (*e*) the same in dorsal view; (*f*) the atlas neural arch in dorsal view; (*g*) the same in right lateral view; (*h*) the same in ventral view; (*i*) the same in anterior view; (*j*) the atlas intercentrum in dorsal view; (*k*) the same in anterior view; (*l*) the proatlas in dorso-lateral view; (*m*) the same in ventro-lateral view. (All three-fifths natural size.) (*n*), (*o*) The odontoid and atlas neural arch enlarged to illustrate atlas rotation. (*n*) Before rotation, the atlas neural arch (broken line) lies with a facet (cross-hatching) over the odontoid facet (stippled). (*o*) The odontoid has rotated, tending to move downwards, laterally and forwards under the neural arch facet of the right hand side.

(figure 36*a*). The neural spine is greatly expanded antero-posteriorly and anteriorly is drawn up into a rugose boss. The posterior zygapophyses are of normal build: they are concave ventro-laterally and orientated at an angle of approximately 40° to the vertical, therefore permitting a degree of both lateral and dorso-ventral movement, as well as some rotation. The anterior zygapophyses are small, flat plates which could possibly contact the posterior extension of the medial wing of the atlas neural arch. This is broken off in the present specimen so contact cannot be established.

Stout, backwardly pointing transverse processes are present. As far as can be seen these bear no distinct rib facets on their distal ends. A distinct facet is present on the centrum, however, projecting laterally from near the ventral margin of the centrum (figure 36*a*: r.f.), although no ribs for vertebrae 1 and 2 were recovered.

From a comparison with modern reptiles, the muscles that must be considered in connection with the atlas–axis complex are the rectus capitis dorsalis major and minor, rectus capitis lateralis, and the obliquus capitis superior, inferior and magnus. In the following, where muscle markings in *D. trigonocephalus* have been equivocal a better preserved specimen, TSK 68, has been used for comparison.

In *D. trigonocephalus* the origin of the rectus capitis dorsalis major, from the anterior rugose boss of the axis neural spine, is quite clear. The origin of the rectus capitis dorsalis minor is not as clear but probably this muscle attached to the dorsal surface of the atlas neural arch between transverse process and lateral process, where there is a possibility of a muscle scar in *Dicynodon trigonocephalus*, and a definite scar in TSK 68. The obliquus capitis superior could have attached to the atlas neural spine, since TSK 68 bears a small but marked fossa in this region.

The attachments of the obliquus capitis inferior are probably the largest of the complex: the origin is from a marked fossa occupying almost the entire lateral surface of the axis neural arch and spine. This fossa has an uneven surface texture and is heavily pitted and striated in TSK 68. The insertion of the muscle is onto the dorsal and possibly antero-lateral surfaces of the transverse process: these areas bear distinct markings in both *D. trigonocephalus* and TSK 68. The obliquus capitis inferior was therefore a substantial muscle pulling the atlas neural arch dorso-medially and posteriorly.

Whether an obliquus capitis magnus was present or not is central to the argument of how much rotation was permitted in the atlas–axis complex, since the attachments of the obliquus capitis magnus would tend to restrict rotational movements. In *D. trigonocephalus* there is a suggestion of a low ridge cutting off the most posterior part of the lateral surface of the axis neural spine. In TSK 68 this is far more distinct: the pitted fossa for the origin of the obliquus capitis inferior ends quite distinctly as a low ridge a short way from the posterior margin of the neural spine. The pitted and striated appearance of the bone continues to the posterior margin and a little way onto the posterior surface of the neural spine. It is not inconceivable, therefore, that this represents an origin for the obliquus capitis magnus, but, as Cluver (1971) supposed, it is reduced compared with the specialized modern reptile condition, and might not have inhibited rotation too much, were this to have occurred.

The ventral surface of the atlas transverse process does bear a small muscle scar. This is probably the origin of the rectus capitis lateralis.

Rotation at the occipital condyle–atlas joint can be ruled out, as Kemp suggests, since the effectively bicondylic arrangement prohibits this; rotation at the atlas–axis joint has already been ruled out. However, two factors above argue for a degree of rotation at the atlas centrum–

neural arch joints. The first is the reduction of the obliquus capitis magnus; the second is the large obliquus capitis inferior. The latter, as noted above, is pulling backwards and dorso-medially. If the head rotates, the atlas neural arch and the occipital condyle must remain fixed relative to one another to maintain the integrity of the spinal column. To produce rotation of the head in an anticlockwise direction, viewed posteriorly, the obliquus capitis inferior of the right side must contract. Also, the articulating surfaces of the neural arch and odontoid must not constrain one another; in other words, the right atlas neural arch must be free to slide over the right odontoid articulatory facet in a strictly anticlockwise path. Such a simplified path is not permitted by the articulating surfaces, however. Instead, because of the morphology of the surfaces, the right atlas neural arch moves backwards and inwards over the right odontoid facet.

The articulating facet on the odontoid is approximately oval, tapering at its anterior end. The posterior half of the facet faces dorsally and is almost flat. The facet then begins to become convex from side to side at the same time as the whole anterior part of the facet is becoming dorso-laterally orientated (figure 36*e*: od.a.). The neural arch facet is more complicated. It is roughly trapezoid, becoming wider posteriorly (figure 36*h*: n.a.). It is concave from side to side over its entire length, more so in its postero-medial corner. The two surfaces are therefore not obviously congruent. Before contraction of the obliquus capitis inferior, the right neural arch rests comfortably on the right odontoid facet, with the transverse process orientated parallel to that of the axis. This orientation means that the neural arch facet lies diagonally along the odontoid facet and the entire surface of the neural arch facet is covered. A postero-lateral portion of the odontoid remains exposed (figure 36*n*). On contraction, the anterior portions of both the neural arch facet and the odontoid facet are firmly fixed relative to one another, since their surfaces are deeply concave and convex, respectively, and fit together closely. However, the more posterior, flatter portions of the facets permit sliding of the right neural arch backwards and inwards on the right odontoid. As the obliquus capitis inferior of the right side contracts the result is a sliding action, with the antero-medial corner of the atlas neural arch pivoting about a point on the anterior margin of the odontoid (figure 36*n*, *o*: ×). The posterior part of the odontoid, previously exposed, is now articulating with the neural arch facet (figure 36*o*). These relative movements of the atlas–axis complex and the occipital condyle produce a degree of anticlockwise rotation of the head, together with turning of the head outwards and upwards.

During this rotation the neural arch moves medially relative to the odontoid. Kemp suggested that postero-lateral movement of the neural arch occurred, which served the purpose of preventing the neural arch occluding the neural canal during rotation. No evidence of this is seen in *D. trigonocephalus*. In fact, whether the neural arches would occlude the canal at all in *D. trigonocephalus* is doubtful. The neural arch is rather a squat structure, and neither its lateral process nor the anterior process are extensive. There is a substantial gap between the arches of either side before rotation. After rotation the lateral process still does not occlude any part of the canal, but the anterior process lies over it. However, between the anterior process and the body of the neural arch is a wide trough of arc-shaped cross-section (figure 36*i*: tro.). The arc is approximately of a circle the same size as the neural canal, and permits the nerve cord to run through unoccluded even during rotation. Rotation would be rather limited. It would stop when the lateral process abutted against the prezygapophysis of the axis.

The well marked proatlas facet on the neural arch has been noted. The proatlas was probably important in stabilizing the occipital–atlas neural arch joint. Under the action of the obliquus capitis inferior there may have been a tendency for the atlas neural arch to be pulled posteriorly enough to be dislocated from the odontoid. There is no bony constraint to this movement. Furthermore, to permit rotation, the atlas neural arch moves inwards. The posterior component of the obliquus capitis inferior is much stronger than the medial component, however, and it is possible that the proatlas acted as a tie to the atlas neural arch, not only preventing excessive backwards movement, but also forming a fixed point about which the atlas neural arch could pivot to enhance the medial component of its motion.

The rotational element of neck movement was small but significant, and was probably used more in feeding than in other behaviour. Use of the neck muscles in tearing and biting food materials is a common feature of the feeding styles of many animals. Rotational movements may be used to bring one side of the mouth or jaws nearer to the food source and to bite and pull repeatedly on it. This might have been true of *D. trigonocephalus*. However, judging by the area available on the occiput for their insertions, other neck muscles, for example the longissimus cervico-capitis and semispinalis capitis and probably the trapezius and cleido-occipitalis, probably played a much greater part in neck movement and support, leaving the much smaller suboccipital musculature to 'fine tune' the muscular activity.

(iii) *The neck region*

Jenkins's (1971*b*) account of *Cynognathus* attempts a reconstruction of the epaxial musculature, based mainly on the work of Vallois (1922) and Olson (1936). Little definite evidence for exact sites of insertion exists in the vertebrae of *D. trigonocephalus*, but it is possible to indicate the approximate position and importance of some muscles. The main muscles for consideration are, of the shorter intervertebral muscles, the interspinalis, and of the longer intervertebral muscles the spinalis, semispinalis, longissimus dorsi and ilio-costalis. The levator costae and anterior serratus muscles will also be included in the discussion.

On vertebra 3 to 7 (figure 37) the transverse processes take the form of stout plates, facing antero-dorsally on vertebra 3 to 5 and then more nearly dorsally on vertebrae 6 and 7. The transverse processes here are the largest in the vertebral column, correlated with the need for strong musculature to support the head. On vertebrae 5 to 7 the antero-dorsal or dorsal surface of the transverse process bears a marked but shallow depression (figure 37*b*: dep.). (The processes of vertebrae 3 and 4 are too damaged to reveal any possible depressions.) These depressions probably mark the insertion of the longissimus dorsi or the longissimus dorsi cervico-capitis. The most elaborate insertion of this muscle is in the neck region, and together with the ilio-costalis cervico-capitis these would form the main lateral head-moving and support muscles. The spinalis capitis is of necessity a smaller muscle because of its limited area of origin, the neural spines of vertebrae 2 to 8. The neural spines of the posterior neck vertebrae are more upright and possibly a little longer than those of the dorsal vertebrae. They are also particularly flattened, and short antero-posteriorly, and while this means that the neck could be flexed upwards so that the animal's head could be held high off the ground, it also cuts down the area for insertion of the spinalis capitis. This is probably not a disadvantage in that muscles like the spinalis act as ties across successive vertebrae and would restrict movement somewhat in an otherwise flexible region.

Vertebrae 3 to 9 bear two separate facets for articulation with the double-headed rib, one on the end of the transverse process and one on the end of the centrum (figure 37*a*: r.f.). As

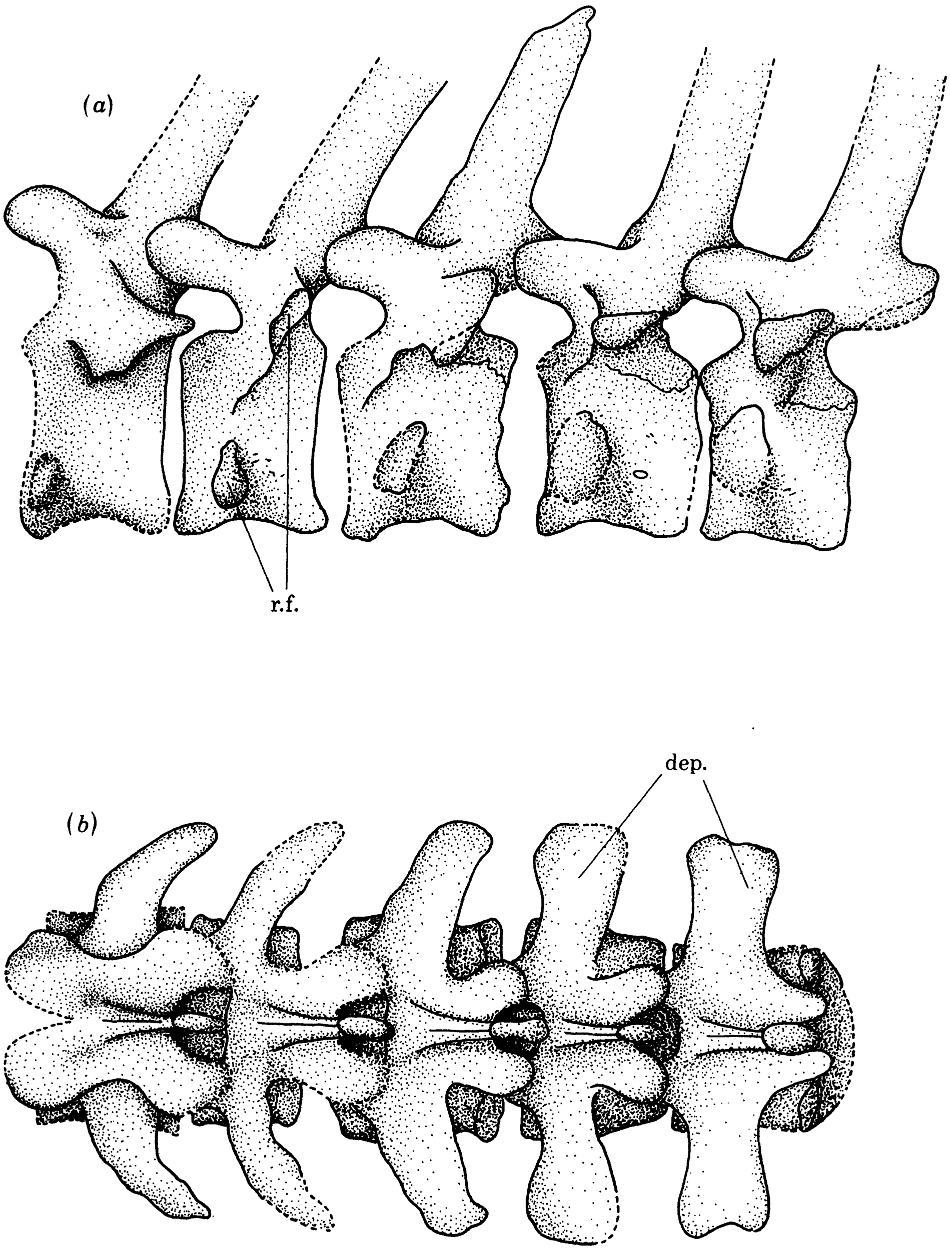


FIGURE 37. Vertebrae 3 to 7 (left to right; natural size): (*a*) left lateral; (*b*) dorsal.

vertebra 9 is approached the centrum facet moves from a ventral position to occupy an area just below the neural arch–centrum suture, whereas the diapophysis moves from the end of the transverse process partly onto the lateral surface of the neural arch. Between the two heads of the cervical ribs is a deep fossa (figure 40*g*: fo.). This fossa is excavated in the postero-medial surface, opening as a notch in the antero-lateral surface of the rib between the heads. The fossa is oblique, suggesting that if anything actually passed through the notch it would do so from a postero-lateral and dorsal direction. It seems unlikely that the fossa was connected with any muscle. It seems more likely that it served to transmit blood vessels or nerves to the musculature of the very robust anterior ribs, which is possibly more extensive (considering the serratus

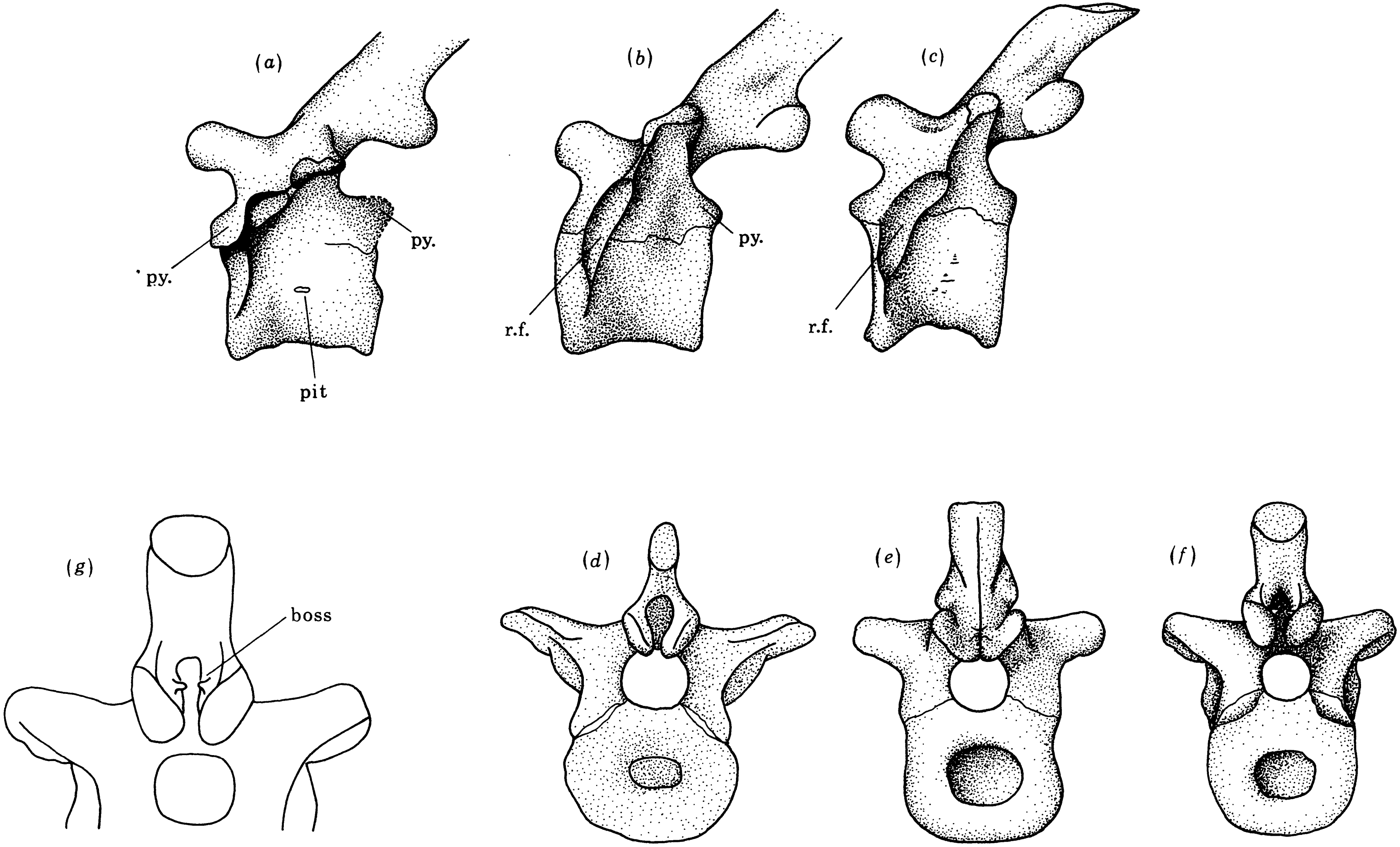


FIGURE 38. (*a*) Vertebra 10 in left lateral view; (*b*) vertebra 16 in left lateral view; (*c*) vertebra 21 in left lateral view; (*d*) vertebra 16 in posterior view; (*e*) vertebra 21 in anterior view, (*f*) vertebra 21 in posterior view; (*g*) enlargement of vertebra 21 to show the posterior zygapophysial bosses. ((*a*)–(*f*), Natural size.)

musculature) than that of the more posterior ribs, and therefore is associated with a special supply of vessels and/or nerves. In rib 6, the fossa is continued over the postero-medial face of the rib head, into the posterior groove seen on all ribs, possibly connected with the attachment of the intercostal muscles. The vessels or nerves passing through the notches must attenuate rapidly after vertebra 10, and certainly the notch and the channel between the head and the body of the centrum all decrease in size through the neck vertebrae.

The neck ribs from vertebrae 6 to 9 bear a pronounced thickening on the anterior surface. Actually these ribs leave the vertebrae postero-laterally so that the anterior surface becomes antero-laterally facing. The centre of this thickening bears a rugose area, which could represent the origin of the anterior serratus muscles. If the anterior serratus superficialis did attach to rib 9 or 10, then it would be able to cause glenoid rotation as postulated in the discussion of the forelimb.

The zygapophyses of the neck vertebrae are particularly well developed, especially antero-posteriorly. The articulatory surfaces of the zygapophyses are orientated at a fairly small angle to the horizontal and presumably permit a good degree of lateral movement, as well as some dorso-ventral flexion and extension. A small degree of rotation of one vertebra about another may be possible but cannot be demonstrated since the neck vertebrae have not been separated during preparation.

The neck is therefore osteologically a flexible region, but also presents firm areas of attachment for the muscles that move and support the massive head. In addition, the cervical ribs are particularly robust to give attachment to the serratus muscles.

(iv) *The dorsal region*

Compared with the neck the dorsal region is characterized by a reduction in flexibility (figure 38). The articulations of the dorsal vertebrae are less flexible. The zygapophyses are reduced and are more vertically orientated. This permits only a small degree of lateral movement, perhaps about 5° to either side of the midline, although much of the movement would be restricted if the zygapophyses are covered in cartilage and this seems likely from their appearance. A large degree of dorsal flexion is permitted by the zygapophyses, as much as 30°. However, ventral flexion is much more constrained, since the faces of successive centra contact one another after movement through only a few degrees. This would presumably be further constrained by the presence of an intervertebral disc. The dorsal region therefore seems designed to limit lateral movements somewhat, without emphasizing sagittal flexion. In fact, there was probably little contribution to the stride by this part of the vertebral column, it having a more important function of supporting the massive thorax suspended beneath it.

The trend towards reducing the zygapophyses of the dorsal vertebrae is contradicted by the last dorsal vertebra, where the posterior zygapophyses are long and broad and almost horizontal (figure 39*a*). This would obviously introduce much more flexibility into the dorso-sacral junction. Such flexibility has been commented on by Gregory (1912), who noted that in running quadrupeds the pelvis is bent, first on one side, then on the other, so that the thrust of the femora is brought more nearly into line with the antero-posterior axis of the body. This would also increase the length of the stride. This has also been suggested by Stillman (1882), in the horse:

> 'The difficulty in locomotion that would be experienced from the want of flexibility of the spine, especially in old-age, is obviated by the freedom of motion that is served in the articulation of the last of the dorsal vertebrae with the sacrum.'

The flexible dorso-sacral joint in *Dicynodon trigonocephalus* may serve the same purposes, of increasing stride length and aligning femoral thrust.

As far as muscle attachments are concerned, the attachments of the shorter intervertebral muscles, which presumably act as strengthening ties between vertebrae, are indistinct. Presumably, though, the interspinalis connected the neural spines of successive vertebrae. The rounding of the neural spines in the mid-dorsal region may reflect a need for increased areas of attachment as this muscle is elaborated, to hold the dorsal vertebrae together more firmly.

The longer intervertebral muscles, the spinalis and semispinalis, longissimus dorsi and iliocostalis again leave no definite mark of their attachment sites. However, if the spinalis and semispinalis occupy similar areas to those in *Dimetrodon* (Olson 1936) then they would seem to aid the shorter intervertebral muscles in holding the column together. Attaching along the neural arches they are too medially placed to cause strong lateral undulatory movements, and also the rather short neural spines would argue against their effectiveness in producing marked dorso-ventral flexion movements.

The transverse processes show variation over the length of the dorsal vertebral region. The antero-posterior width of the transverse process begins to decrease after vertebra **9**. This is correlated with two other trends: first, that the transverse process does not leave the body of the vertebra transversely, but instead faces antero-dorsally; and secondly, that while the transverse processes of the anterior vertebrae stand proud of the neural arch, the anterior surface of the neural arch of the more posterior vertebrae gradually expands laterally to fill in the angle between the process and the body of the neural arch, as seen in anterior view (compare figure 38*b*, *d* with figure 39*c*). As a result of these three trends, the transverse processes of vertebrae **25** and **26** are extremely narrow (front to back) plates, leaving the neural arch in an almost vertical plane, but not extending as processes distinct from the body of the neural arch. Vertebra **26** also shows the unusual feature of slightly forwardly turned transverse processes. These bear a marked ridge along their postero-dorsal edge (figure 39*c*: r.).

The longissimus dorsi is usually reconstructed with an origin on the anterior dorsal edge of the internal surface of the ilium, inserting on the dorsal or antero-dorsal aspect of the transverse processes and also the rib heads. If one assumes that this is largely correct, although there is no direct morphological evidence for it in *D. trigonocephalus*, then the following observations may be made.

As noted above, the transverse processes begin to slope anteriorly and to decrease in their antero-posterior length after vertebra **9**. This trend to decrease in length is continued through to the sacral vertebrae and so presumably the slips of the longissimus dorsi become weaker more posteriorly. This would be consistent with the fact that the posterior dorsal vertebrae do not have a great degree of lateral movement, because of their vertical zygapophyses. In *Dimetrodon*, Olson (1936) reconstructs the longissimus dorsi insertions as being on the dorsal surface of the transverse processes and continuing down onto the dorsal surface of the rib head. This continuous insertion is possible in *D. trigonocephalus* only in the anterior vertebrae, where the rib head articulates with the end of the transverse process. More posteriorly the rib facet is on the ventro-lateral surface of the transverse process and the anterior border of the lateral face of the centrum (for example figure 38*b*, *c*: r.f.), and so the rib is separate from the end of the transverse process and some millimetres below and in front of it. It would seem, then, that, apart from in the cervical region, the insertion of the longissimus dorsi could not have been as indicated in *Dimetrodon*. Either the insertion had been reduced and confined just to the dorsal

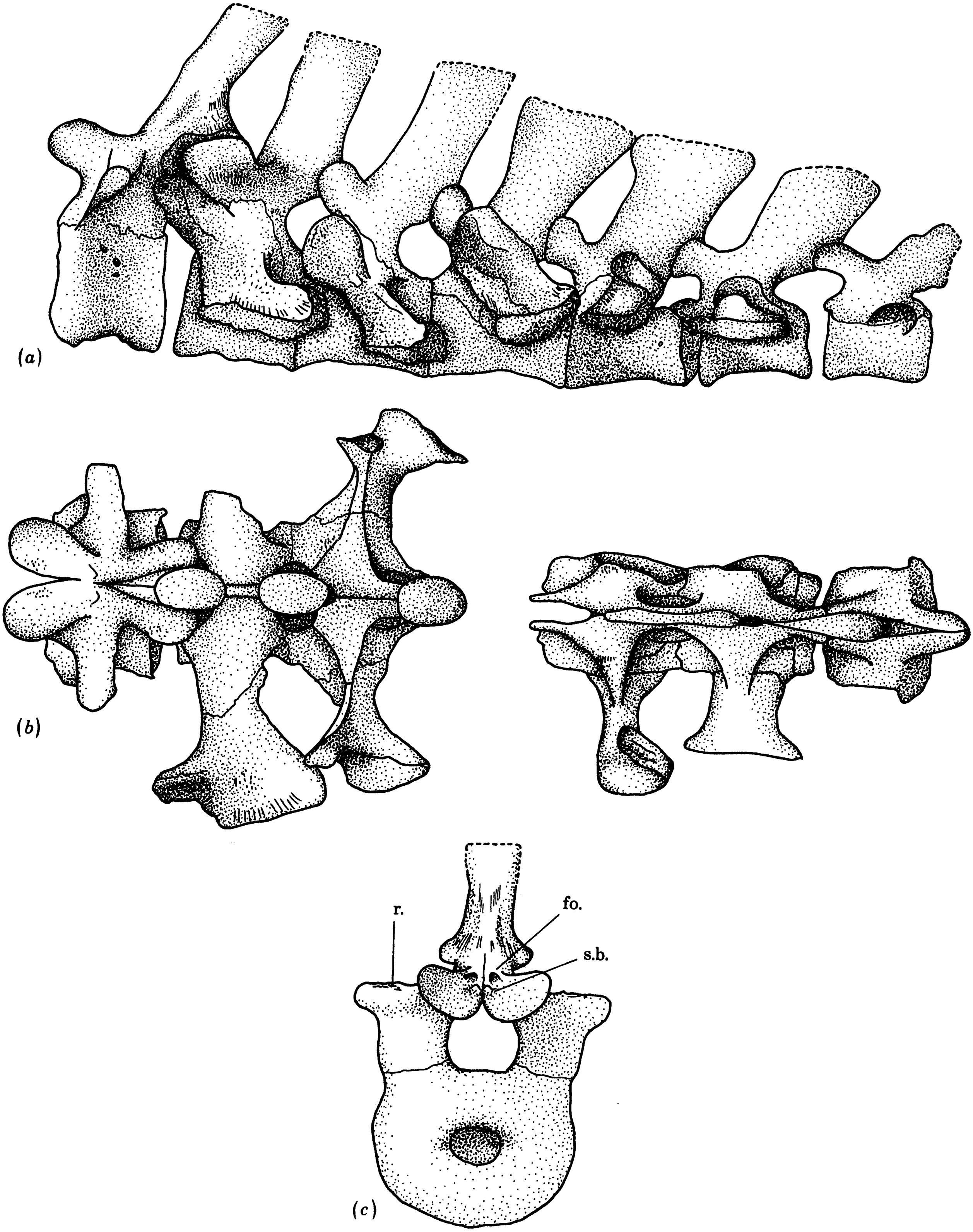


FIGURE 39. Vertebrae 26 to 32 (left to right; natural size): (*a*) left lateral; (*b*) dorsal; (*c*) vertebra 26 anterior.

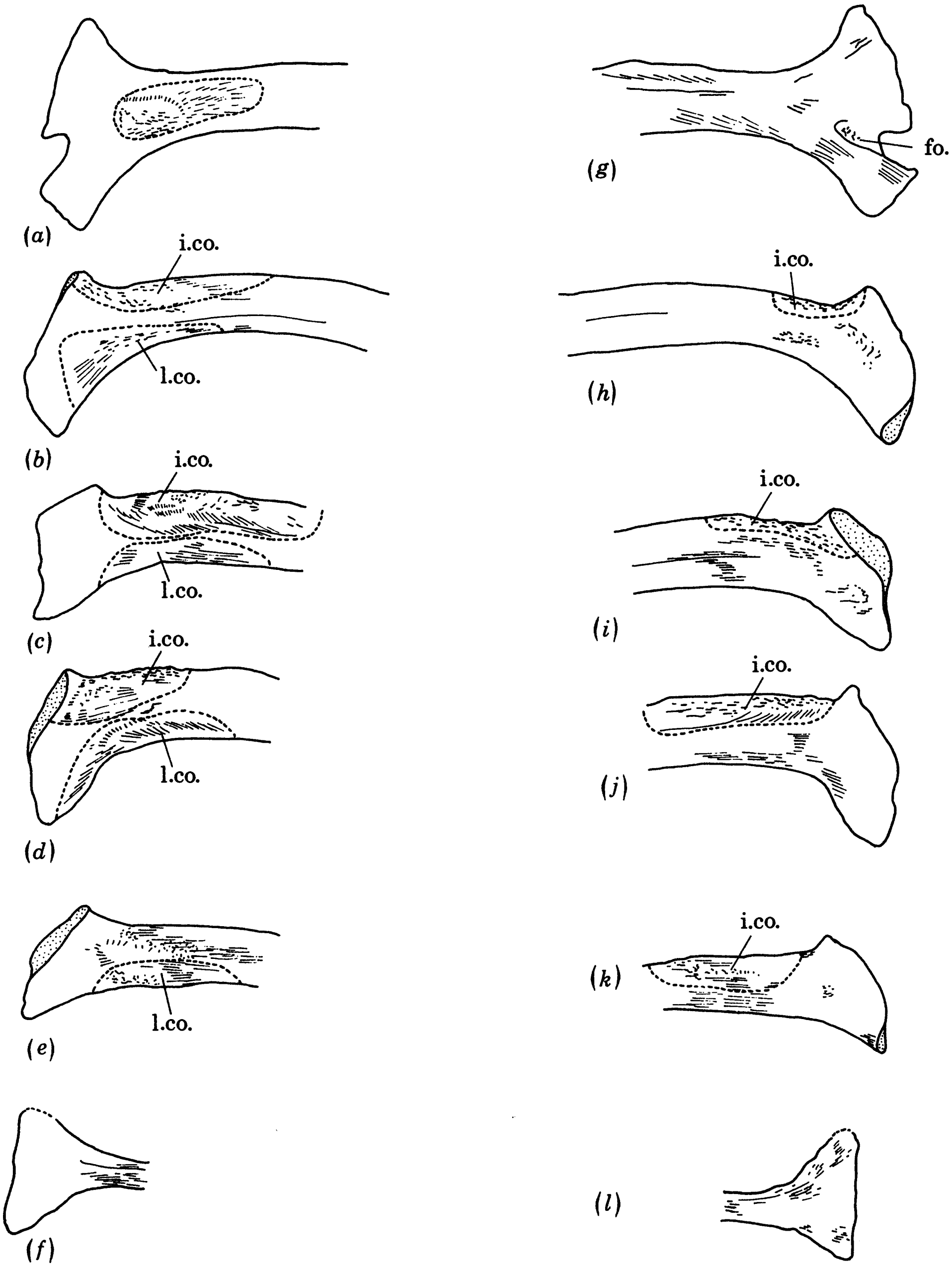


FIGURE 40. The ribs (magn. × 1): (*a*)–(*f*) posterior view; (*g*)–(*l*) anterior view; (*a*), (*g*) rib 7; (*b*), (*h*) rib 11; (*g*), (*i*) rib 15; (*d*), (*j*) rib 19; (*e*), (*k*) rib 23; (*f*), (*l*) rib 26.

surface of the transverse process, or else the muscle may have inserted in two distinct slips, one onto the transverse process and one onto the rib head. Which of the two alternatives is more likely to be correct can be judged from considering the attachment of the longissimus dorsi and other muscles to the ribs. The muscles in question (according to Olson (1936)) are, in the neck region, the longissimus cervico-capitis and ilio-costalis cervico-capitis, and, more posteriorly, the longissimus dorsi, ilio-costalis dorsi, the levator costae and the intercostal muscles. To these must be added, in the shoulder region, the serratus muscles (Romer 1922), whose origins are on the antero-dorsal surfaces of the distal parts of the rib stems. The serratus anterior superficialis has been given special consideration in *D. trigonocephalus*; this muscle would probably originate from the ribs of vertebrae 9 and 10.

A sequence of rib heads, each bearing a few centimetres of stem, were examined to plot the various patches of foramina and striations, which are pronounced (figure 40). The ribs are from the 7th vertebra (left side), the 11th vertebra (right side), the 15th vertebra (right side), the 19th vertebra (left side), the 23rd vertebra (right side) and the 26th vertebra (left side). Within this sequence the following trends are visible. The ribs are fairly robust until vertebra 20, when they become rapidly smaller towards vertebra 26. In particular they become very much narrower antero-posteriorly. Similarly the rib stem decreases and becomes very slender from vertebra 18 to vertebra 26.

From examining the rib sequence it can be seen that the dorsal ribs show two main areas that are possibly muscle scars. One is a rugosity along the dorsal edge of the rib, from the head, along the stem (figure 40: i.co.). In more posterior ribs it also encroaches on the posterior surface. The dorsal rugosity is most pronounced in the ribs of vertebrae 10 to 20. On rib 23, the rugosity itself is less marked but the marked area on the posterior surface of the rib is greater.

The second possible scar is on the anterior surface of the head of the rib, near the ventral edge (figure 40: l.co.). The scar may extend along the rib stem for a short distance. The area is pitted and uneven in texture. It is most marked in rib 11.

These two areas most likely represent the insertions of the ilio-costalis and levator costae, respectively (figure 40: i.co., l.co.). The ilio-costalis is chosen rather than the longissimus dorsi because the muscle scar area extends all along the rib stem, as seen in the longest rib available. The levator costae has a strong insertion on those ribs of the thoracic region, but gradually diminishes from rib 21 onwards until it is indistinguishable on the last dorsal rib. The neck ribs do not have obvious insertional areas for this muscle, either.

In conclusion, the markings on the rib heads and stems give no indication of a longissimus insertion. Although this insertion cannot be ruled out it is possible that the longissimus was confined to the dorsal surface of the transverse process, and was therefore reduced from the primitive condition.

The last long intervertebral muscle for consideration is the ilio-costalis. It seems that its insertions were along the dorsal edges of the rib heads and stems. Its origin was presumably on some part of the pelvic girdle. It must be assumed that in *D. trigonocephalus* the ribs had a considerable degree of freedom from the vertebrae. No rib is fused to its articulation with the vertebra, and after the neck region there is no longissimus dorsi overlapping the transverse process and rib head, which would presumably have added some rigidity to that junction. In this situation, the action of the ilio-costalis on the ribs must have been somewhat modified over the primitive condition, because there would be a tendency on unilateral contraction of the ilio-costalis to dislocate the ribs of the relevant side, rather than produce unilateral movement of the body. However, if the pull of the ilio-costalis could be balanced by the levator costae of each rib, then the bilateral contraction of the ilio-costalis and contraction of the levator costae muscles could lead to the positions of the ribs remaining fairly fixed, therefore helping to cut out lateral undulation.

Judging by the size decrease of the relevant areas, both ilio-costalis and levator costae insertions are reduced more posteriorly in the vertebral column, which is consistent with the fact that more flexibility is required in the immediate presacral region, as outlined before.

(v) *The sacral region*

There are five sacral vertebrae, that is, vertebrae having ribs that abut the ilium (figure 39). The centra of the first four are fused together. The fifth is free.

Both anterior and posterior zygapophyses are reduced considerably in the sacral region. The anterior zygapophyses of sacral vertebra 1 are probably the largest in the spinal column, to articulate with the greatly elaborated posterior zygapophyses of vertebra 26, as noted. However, after this the zygapophyses become vertically orientated and extremely narrow transversely. But their length and height are not reduced; both become greater in sacral vertebrae 4 and 5. The anterior and posterior zygapophyses of the posterior sacral vertebrae may indicate a certain amount of fusion. The zygapophyses of the first caudal vertebra are more robust and plate-like.

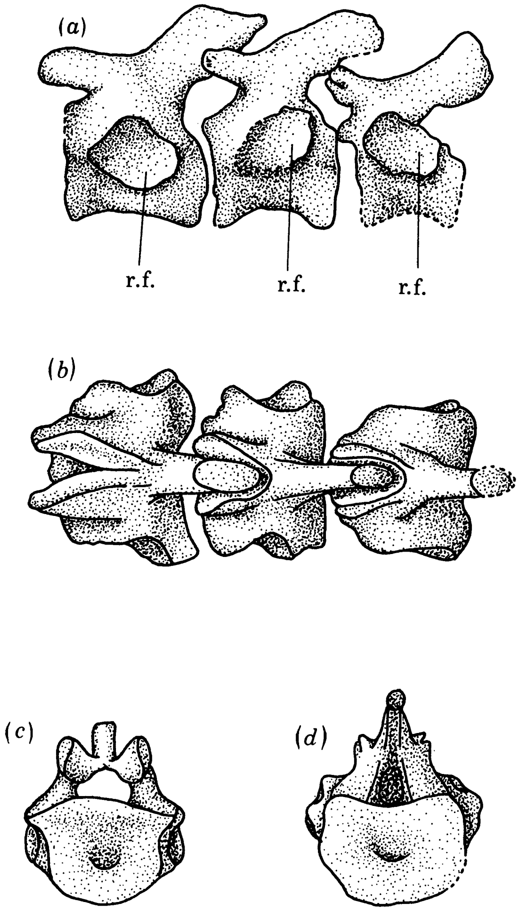
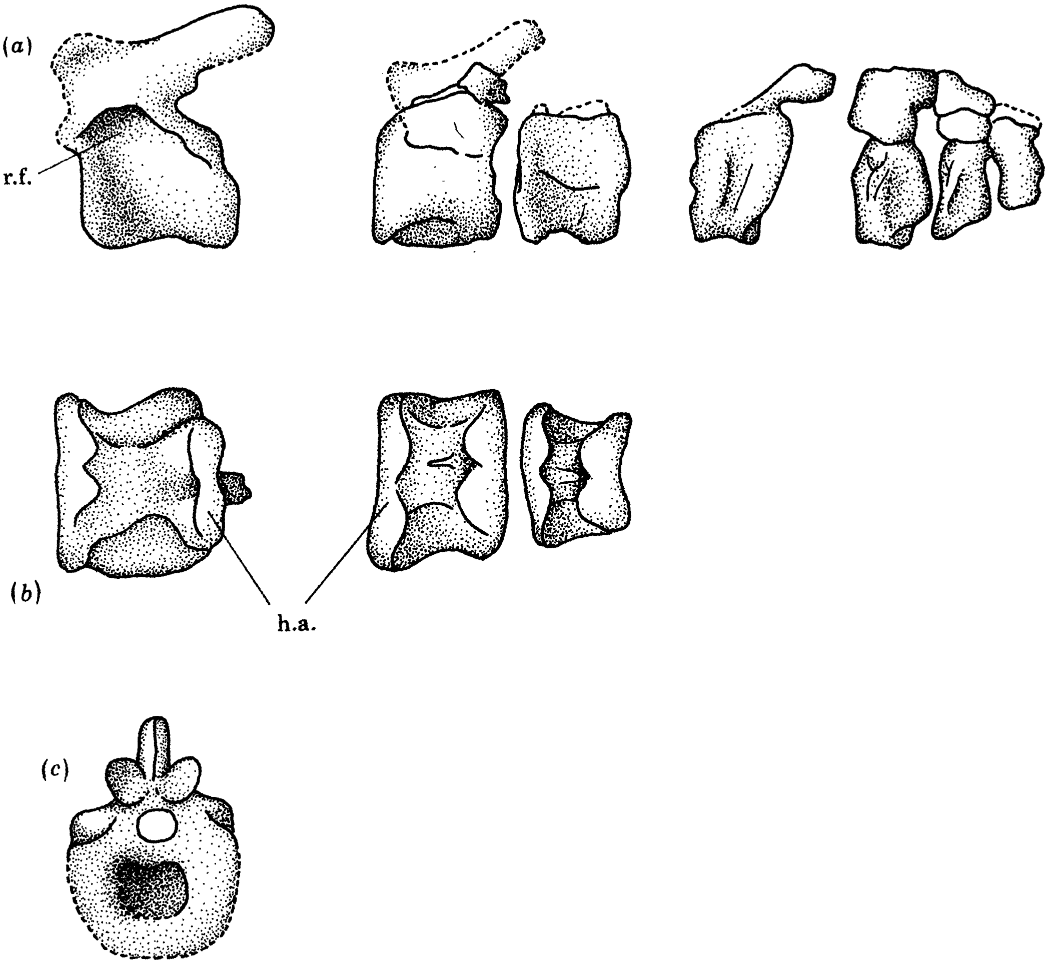


Figure 41. Vertebrae 33 to 35 (left to right; magn. × 1): (*a*) left lateral; (*b*) dorsal; (*c*) vertebra 33 anterior; (*d*) vertebra 33 posterior.

The sacrum, then, takes the form of a strong, rigid rod of bone, to support the pelvic girdle.

The neural spines of the sacral vertebrae make an angle of about 20° to the vertical. They also decrease in side to side width, but increase greatly in antero-posterior length. In particular the neural spines of the third, fourth and fifth sacral vertebrae are extremely elongate antero-posteriorly (figure 39*a*). This may provide an area for the origin of the caudal extensor usculature, which would therefore still be reasonably powerful for the rather short tail. The de-to-side flattening, on the other hand, might reflect reduction of the attachment of the interertebral muscles, because they are not relied on for maintaining the integrity of the sacrum, is being accomplished by fusion of the centra and the zygapophyses.

The sacral ribs are all expanded. They are not fused to the centrum rib facets, but seem to ticulate normally. As explained previously, ligamentous connections probably stabilized the cro-iliac joint, possibly introducing a degree of flexibility.



IGURE 42. Vertebrae 36, 38, 39, 41, 43 to 45 (left to right: magn. × 1½): (a) left lateral; (b) ventral; (c) vertebra 36 anterior.

i) *The caudal region*

Parts of twelve and possibly thirteen caudal vertebrae exist, although after the third caudal ertebra preservation of the bone varies and may be poor (figures 41, 42).

The length and diameter of the centra gradually diminish towards the tip of the tail, which probably complete.

Large facets for articulation of the much reduced ribs can be seen clearly up to caudal ertebra 5 (figures 41, 42*a*: r.f.): this is also the last vertebra for which ribs are known in the present specimen (figure 43). After this the state of preservation of the bone does not allow firm identification of the rib facets.

Facets for the reception of the haemal arch can be seen from caudal vertebra 6 onwards (figure 42*b*: h.a.). Only one haemal arch is preserved, probably that of caudal vertebra 9.

The neural spines decrease in height along the tail, and appear to be more backwardly directed than those of the dorsal vertebrae.

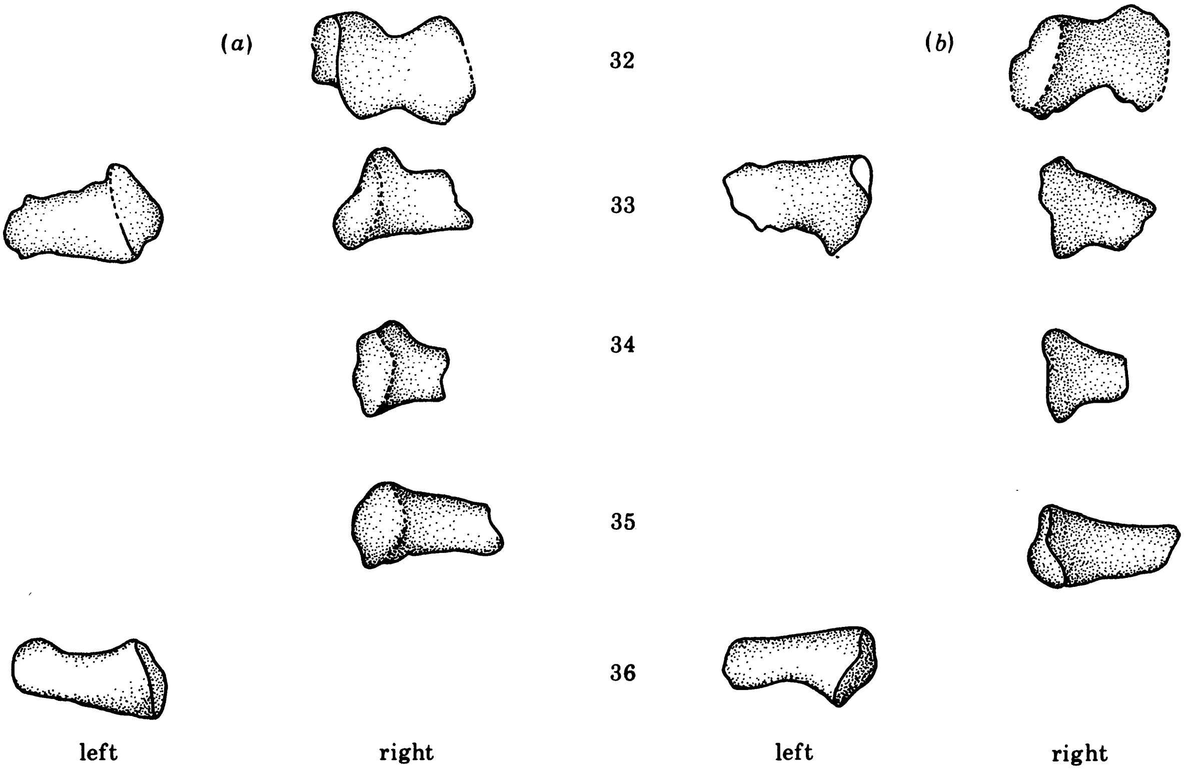


Figure 43. The ribs of vertebrae 32 to 36: (*a*) ventral; (*b*) dorsal. (Magn. × 1½.)

Since the caudal vertebrae diminish rapidly in size towards the tip of the tail and have both reduced neural spines and transverse processes, the tail was presumably lightly built and does not seem to have provided an extensive origin for the caudi-femoralis muscle.

(vii) *Conclusions*

It seems that the axial skeleton did not play a large part in producing locomotory force: lateral undulation was not a significant component of the stride. Indeed, certain features of the axial skeleton may be adaptations towards eliminating lateral undulation.

Discussion and summary

From the study of the postcranial skeleton of *Dicynodon trigonocephalus* the following conclusions were made.

The forelimb takes up a sprawling position, producing a wide trackway. No muscles were positioned so as to produce a powerful locomotory force, but strong adductors and elevators help to prevent dislocation, and make the shoulder joint strong and stable. In connection with this, the glenoid permits adequate contact of the head of the humerus throughout the protraction–retraction arc, and long axis rotation. The antebrachium is rather short, but this might add to stability by keeping the centre of gravity low, or might merely indicate that with a slow, controlled stride a longer limb is of little advantage.

The hindlimb is in a semierect position throughout most of the stride and could produce a powerful, but not rapid, locomotory force. Much of this force is generated through long axis rotation of the femur. Reliance on long axis rotation is caused by the small degree of protraction–retraction possible, because the extensive areas of muscle attachment on the femur necessitate extensive processes on the bone, which collide with the acetabulum margins after a small excursion. The areas of muscle insertion seem of necessity to be large because *D. trigonocephalus* is a fairly large animal, retaining a basically reptilian muscle arrangement and therefore relying on powerful postural musculature to prevent collapse of the body.

The importance of the obturatus internus in femoral retraction, and the reduction of the caudi-femoralis and pubo-ischio-femoralis externus as the hindlimb is turned in towards the body were noted.

The possibility of movements within the pelvic girdle was noted, and also the rather weak pubo-ischiadic symphysis. A positive explanation of these features is still lacking, although it has been suggested (Watson 1960) that the weak symphysis permitted egg-laying. However, this would apply equally to the bearing of live young. It would seem unlikely that a great degree of movement between the parts of the girdle was permitted, since the girdle must resist the considerable force of the locomotory muscles.

Concerning the axial skeleton, it was concluded that the spinal column had become more rigid, by osteological and musculature changes, and that lateral undulation of the body had been cut down. Possibly, in a large animal with a bulky thorax and abdomen, lateral undulation would be limited in any case. However, this reduction of lateral undulation would affect locomotion in that, all else remaining equal, length of stride would be decreased. Normally, during lateral undulation, as the limb is protracted the body is convex on the side of the limb, throwing it further forward. Similarly, as the limb is retracted, if the body is concave on the side of the limb, this will be thrown further back. These actions therefore increase the stride. As lateral undulation is reduced in *D. trigonocephalus*, it is possible that long axis rotation took over as a means of lengthening the stride, by allowing increased anterior excursion of the crus. Also rotating the retracted femur with the crus fixed on the ground will throw the body anteriorly a little further, assuming that excursion of the crus is postero-lateral, rather than just lateral. It is interesting that in the forelimb, where long axis rotation is rather limited, yet another way of increasing the stride, namely glenoid rotation, is used.

Reduction of lateral undulation, presumably in an attempt to improve locomotory efficiency, and possibly because the bulk of the body interfered with it, therefore had important consequences on the rest of the locomotory pattern.

In contrast to the dorsal axial skeleton, the neck was probably flexible, permitting various movements, including a degree of rotation, but it was also the attachment area for the occipital muscles. Judging by the area available for their origin on the occiput, these must have been extensive, and probably played an important role in feeding behaviour. The neck vertebral muscles themselves (longissimus cervico-capitis and ilio-costalis cervico-capitis) were also extensive to strengthen the neck to support the massive head.

These conclusions suggest a slow-moving but powerful animal, whose locomotion had progressed beyond the presumably primitive reptilian condition of relying on a sprawling gait and lateral undulation. These advances, however, were not necessarily in any way towards a 'mammalian' condition. After developing key innovations such as shortening of the snout, a movable quadrate and a jaw hinge that permitted propalinal movements, dicynodonts evolved independently of all other therapsids (King 1979) except possibly dinocephalians. The characters of dicynodonts that appear to be 'mammalian', for example reduction of the caudi-femoralis, will probably be found to occur in the earliest therapsids (eotitanosuchids, phthinosuchids), at least incipiently, and therefore be characters primitive to all therapids.

Being a slow-moving herbivore, *D. trigonocephalus* may have depended on crepuscular or cryptic behaviour to escape predators. Having the possibility of a fairly powerful, but not rapid, locomotory mechanism might also indicate that the animals were adapted for endurance rather than speed, possibly for food-finding expeditions. Keyser (1970) considers that the *Cistecephalus* zone environment probably consisted of a vast plain, traversed by streams, along which flora and fauna would have been concentrated. Between periods of flooding, the plain would have been very dry, and excursions between streams for the animals concerned would have been arduous.

No specialized habits such as digging or water-dwelling are indicated by the analysis of the postcranial skeleton.

Study of the skull throws further light on the possible habits of *D. trigonocephalus*. Compared with *Oudenodon* the skull is capable of a wide gape and is supplied with powerful adductors (see below). The power of its jaws and muscles suggests that it fed on tough plant matter such as the rhizomes and woody stems of equisetalians, possibly felling such plants before utilizing them as a food-source. Propalinal jaw movements producing a grinding action would lead to comminution of this tough material. *Oudenodon* could not have exploited such a food source, relying rather on the softer leaves and shoots of the larger plants available.

It has been suggested earlier that *D. trigonocephalus* might have had improved vision but a reduced sense of smell. This might suggest a crepuscular or cryptic habit again, with the necessity to compensate for a fall in light intensity and lack of odour transmission in a wooded environment. This would be consistent with the slow, powerful gait.

RELATIONSHIPS OF *DICYNODON TRIGONOCEPHALUS*

From an analysis of the cranial structure it is apparent that many differences exist between *D. trigonocephalus* and a more generalized dicynodont such as *Oudenodon*. Some of the general differences were mentioned in the diagnosis: skull width greater than skull length; postorbitals overlapping the parietals on the skull roof; labial fossa present; shortened basicranial axis. These modifications of the skull can be seen to have the following consequences on the arrangement of the jaw muscles relative to *Oudenodon*:

(1) the fibres of the adductor externus lateralis are longer and more parallel to one another, giving a more vertical pull and possibly a wider gape;

(2) the pull of the adductor externus lateralis is slightly less lateral because the muscle is inserted into the lateral dentary ledge;

(3) the adductor externus medialis also has longer fibres;

(4) the anterior pterygoideus has shorter fibres, and the posterior pterygoideus a more medial pull.

These differences are a consequence of shortening and deepening the skull from an

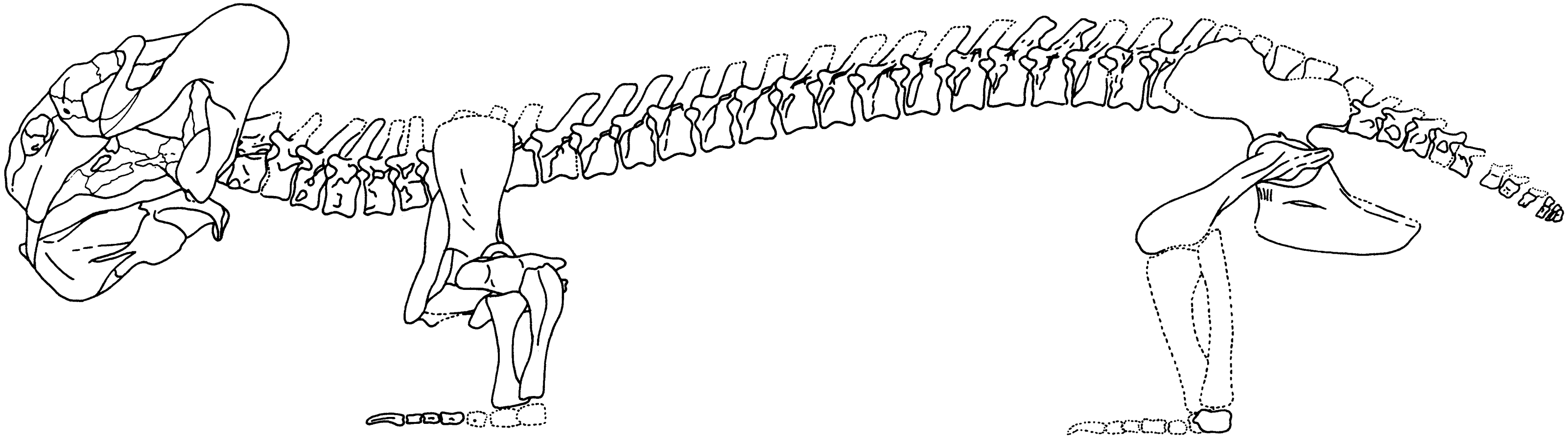


FIGURE 44. A reconstruction of the skeleton of *Dicynodon trigonocephalus*. (Approximately one-fifth natural size.)

Oudenodon-like condition. To be precise, the snout is deepened, the skull length reduced and the temporal region deepened. Probably the biggest functional difference that this would make to the skull would be in the gape allowed. *D. trigonocephalus* could have achieved a proportionally larger gape than *Oudenodon*. This would imply that its food material was much more substantial than that of *Oudenodon*.

The changes that have occurred in the skull configuration of *D. trigonocephalus* are similar to those that have occurred in the skull of *Lystrosaurus*, as Cluver indicates. *Lystrosaurus* is, of course, a basal Triassic form and Cluver attempts to trace its ancestry from a Permian form. He gives several characters that *Lystrosaurus* exhibits, some of which are peculiar to *Lystrosaurus* and some of which are shared by other Triassic genera.

The unique *Lystrosaurus* characters are:

(1) presence of an intertuberal ridge on the basisphenoid;
(2) the shortened temporal fenestra;
(3) the down-turned snout;
(4) the deepened skull;
(5) the pterygoid contact with the maxilla;
(6) presence of a labial fossa;
(7) the maxillary rim for the slicing of food during mastication.

The shared Triassic features are:

(8) a reduced interpterygoid vacuity;
(9) a reduced ectoterygoid;
(10) the absence of a floccular fossa;
(11) the posteriorly placed parasphenoid and presphenoid.

Of these characters, (1) to (3), (6), (8), (9) and (11) are definitely present in *Dicynodon trigonocephalus*. There is no reason why (7) should not occur. Character (10) cannot be determined in the present specimen, and (5) may be incipient. So, between 8 and 10 of Cluver's characters occur in *D. trigonocephalus*.

Whether the similarity is due to parallelism or a close relationship is difficult to determine. Cluver accounts for the change in skull proportions in *Lystrosaurus* by that animal's aquatic nature and by the adoption of feeding on underwater material. He sees the deepening and shortening of the skull as an adaptation to feeding at a lower level while maintaining a large gape. As stated, there is no evidence, either cranial or postcranial, for aquatic habits in *D. trigonocephalus*. The evidence for *Lystrosaurus* being aquatic is rather equivocal but even the few indications of this life style, namely the extended ischium, the shallow ventral region of the pelvis and the long and powerful sacrum, are not present in *D. trigonocephalus*.

It seems likely, however, that selection for a large gape and powerful jaw muscles would increase as dicynodonts began to increase in size during the Upper Permian, to be able to feed efficiently on large and tough plant matter, avoiding competition with smaller forms. It is interesting then, that many *Daptocephalus* zone forms (*sensu* Kitching 1977) show the shortening and broadening of the skull seen in *D. trigonocephalus*, whereas the distinguishing feature of *Lystrosaurus*, snout deepening, is not apparent, except incipiently in *D. trigonocephalus*.

It is possible to say, then, that in the *Daptocephalus* zone dicynodont fauna there were large members, including *D. trigonocephalus*, maximizing gape and muscle force by shortening and broadening the skull. It is possible to envisage a *Lystrosaurus*-like form being derived from such members, though not necessarily directly via *D. trigonocephalus*. The incipient snout-deepening seen in this species may nevertheless indicate that it is the *Dicynodon* species closest to *Lystrosaurus* presently known.

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List of symbols and abbreviations used in the figures

ac.	access to the reflected lamina of the angular
ac.p	acromion process
add.	adductor femoris muscles
a.e.	anterior edge of the reflected lamina of the angular
a.e.l.	adductor externus lateralis
a.e.m.	adductor externus medialis
a.f.	acetabular facet
a.i.f.	anterior section of the ilio-femoralis muscle
ang.	angular
a.p.	anterior pterygoideus muscle
a.p.n.	anterior process of the atlas neural arch
art.	articular
b.	boss
b.a.	body of the angular
bd	band of striations on the radius
bi.br.	biceps and brachialis muscles
bo.	basioccipital
b.p.	bulb-like process of the quadrate
bs.	basisphenoid
bu.pal.	bulbous portion of the palatine
c.	coracoid facet of the glenoid
c.b.	coraco-brachialis muscle
ch.	channel on the stapes
cl.	clavicle
cor.	coracoid
c.1 c.2	circular foramina through the dentary symphysis
d.c.	delto-pectoral crest
d.e.	distal end
del.	deltoideus muscle
den.	dentary
dep.	depression
d.f.	fossa dorsal to the acromion process
d.g.	gap between the dentary and splenial
d.s.	lateral dentary shelf
e.	edge of the ilium
ect.	ectoptergoid
e.f.	elongate foramen on the septomaxilla
eo.	exoccipital
epi.	epipterygoid
fem.	femur
fo.	fossa
for.	foramen
fp.	footplate of the quadratojugal

fr.	frontal
g.	gap between splenial and prearticular
gl.	glenoid
gr.	groove
h.	head
h.a.	haemal arch facet
hum.	humerus
i.c.	opening for the internal carotid artery
i.ch.	internal choana
i.co.	attachment of the ilio-costalis muscle
i.fe.	intramandibular fenestra
il.	ilium
im.c.	intramandibular cavity
ip.	interparietal
ip.f.	interparietal foramen
isc.	ischium
is.f.	ischial facet
i.t.	ischio-trochantericus muscle
j.f.	jugular foramen
ju.	jugal
k.	keel
l.	ledge
l.a.	reflected lamina of the angular
lac.	lachrymal
la.f.	lachrymal foramen
l.c.	lateral condyle
l.co.	attachment of the levator costae muscle
l.cv.	low convexity on the coracoid
l.d.	latissimus dorsi muscle insertion
l.f.	labial fossa
l.p.	lateral process of the atlas neural arch
l.p.f.	lateral palatal fenestra
l.t.	low tubercle on the femur
m.c.	median condyle
m.f.	medium foramen
m.j.c.	maxillary–jugal cavity
mx.	maxilla
mx.sp.	spur of the maxilla
n.	notch
n.a.	neural arch articulation
nas.	nasal
n.f.	proatlas facet which contacts the neural arch
n.1 n.2	notches on the ilium
od.a.	articulating facet on the odontoid
o.f.	proatlas facet to contact the occiput
o.p.	olecranon process
o.r.	oval rugosity on the ulna
os.	orbitosphenoid
pal.	palatine
par.	parietal
pc.	procoracoid
p.cha.	premaxillary channel
pec.	pectoralis muscle
pf.	prefrontal
p.i.	prootic incisure
p.i.f.	posterior section of the ilio-femoralis
p.i.f.e.	pubo-ischio-femoralis externus
p.i.f.i.	pubo-ischio-femoralis internus
pin.	pineal opening
pl.	plate of the quadratojugal
pmx.	premaxilla

po.	postorbital
pof.	postfrontal
p.p.?	possible insertion of the posterior adductor
p.p.f.	pterygo-paroccipital foramen
p.pr.	paroccipital process
pr.	facet on the atlas neural arch for the proatlas
pre.	prearticular
prep.	preparietal
pro.	prootic
ps.	parasphenoid
pter.	pterygoid
pt.	posterior pterygoideus muscle
p.t.f.	post-temporal fenestra
pu.	pubis
pu.f.	pubic facet
pu.t.	pubic tubercle
py.	pyramidal extension of the neural arch
p.VII	palatine branch of the seventh nerve
q.	quadrate
qj.	quadratojugal
qj.f.	quadratojugal foramen
q.r.	quadrate recess
q.r.p.	quadrate ramus of the pterygoid
r.	ridge
rad.f.	facet for the articulation of the radius
r.c.t.	root of the canine tusk
r.f.	rib facet
r.p.	rugose plate
ru.f.	rugose facet for the radius
rug.	rugosity
s.b.	small boss
s.c.	scapula convexity
sc.a.	articulation of the procoracoid with the scapula
scap.	scapula
sco.sc.	subcoraco-scapularis and subscapularis muscle attachments
s.f.	facet for the sacral rib
s.fo.	small foramen in the septomaxilla
s.g.	semicircular groove on the scapula
s.gr.	shallow groove on the septomaxilla
s.h.	scapulo-humeralis muscle attachment
sh.f.	shallow fossa on the reflected lamina of the angular
smx.	septomaxilla
so.	supraoccipital
so.f	supraoccipital foramen
sp.	spoon-shaped proximal end of the clavicle
spl.	splenial
sq.	squamosal
s.r.	splenial recess
st.	stapes
str.	strip of striations on the ulna
sup.	supracoracoideus muscle attachment
sur.	surangular
tab.	tabular
tr.	triangular groove on the coracoid
tri.	attachment of the triceps muscle
tr.m.	trochanter major
tro.	trough on the atlas neural arch
tv.p.	transverse process
ul.f.	facet for the articulation of the ulna
v.c.l.	vena capitis lateralis channel
vo.	vomer
w.ch.	wide channel

×	pivot of the atlas neural arch on the odontoid facet
I	passage of nerve I
II	passage of nerve II

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