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The Primitive Cynodont Procynosuchus: Structure, Function and Evolution of the Postcranial Skeleton

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THE PRIMITIVE CYNODONT *PROCYNOSUCHUS*: STRUCTURE, FUNCTION AND EVOLUTION OF THE POSTCRANIAL SKELETON

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An almost complete, acetic acid prepared skeleton of *Procynosuchus delaharpeae* Broom, an Upper Permian cynodont, is described. The axial skeleton is primitive in lacking the expanded costal plates, and accessory zygapophyses of later cynodonts. The mechanism of the shoulder joint is interpreted, and it indicates that no significant locomotory forces were generated by the forelimb. The hindlimb was capable of both a sprawling and an erect gait. Specialized horizontal zygapophyses in the lumbar region, and other features, show that proficient aquatic locomotion also occurred.

As a representative of a stage in the origin of the Triassic cynodonts, *Procynosuchus* indicates that the dual-gait mechanism of the hindlimb was functionally intermediate between a primitive sprawling gait and the obligatory erect gait of the later cynodonts.

A. INTRODUCTION

This paper is the second part of the study of a specimen of the Upper Permian cynodont *Procynosuchus delaharpeae* from the Luangwa Valley, Zambia. The first part (Kemp 1979) concerned the skull, and also contained a discussion of the phylogenetic position of *Procynosuchus*. The postcranial skeleton is described here, and an attempt is made to interpret it in functional terms. It is also considered in an evolutionary context.

Only the most general aspects of the *Procynosuchus* postcranial skeleton are so far known. Broom (1948) gave a very sketchy account of a skeleton referred to the probably synonymous *Leavachia* (see Hopson & Kitching 1972). Later, Brink & Kitching (1953) refigured this specimen and commented on a few minor errors in Broom's account, but again failed to produce an adequate description. Brink (1951) had also described briefly a second specimen of a postcranial skeleton of '*Leavachia*', consisting of the anterior half. Of other Upper Permian cynodonts, Konjukova (1946) has given a brief note and rather poor figure of the pelvic region of the Russian form *Dvinia*.

The present work has been facilitated greatly by the excellent, detailed review of the postcranial skeleton of the African Triassic cynodonts by Jenkins (1971). The descriptive sections that follow are largely in the form of comparisons of the *Procynosuchus* structure with that of typical cynodonts. Except where otherwise indicated, the standard cynodont condition quoted may be assumed to be based on Jenkins's account.

The skeleton occurred in a single, calcareous mudstone nodule, broken into several pieces, and with a number of fragments already weathered out. The larger pieces, containing articulated runs of vertebrae and ribs, were coated separately over the ventral and lateral sides with thick 'Vinalak'. Complete preparation of each piece from the dorsal side, with the use of acetic acid, permitted extraction of the bones. As with the skull (Kemp 1979), the postcranial bones were covered with a thin layer of the zeolitic mineral heulandite. Although insoluble in acetic acid, this substance had softened sufficiently to be removable using butanone and fine brushes and needles. Despite the very time-consuming nature of the preparation, it proved fully justified by the extremely fine detail exposed.

The axial skeleton is effectively complete, apart from at least one sacral vertebra, and some of the caudals. Of the appendicular skeleton, the only element completely unrepresented is the hind foot, although only parts of the radius, ulna, interclavicle and pubis are preserved. The one remaining forefoot lacks the phalanges.

Locality. Site 2C, Middle Luangwa Valley, Zambia (Kemp 1975).

Horizon. Madumabisa Mudstones, equivalent to the *Daptocephalus*-zone of the South African Karroo. Upper Permian.

Field no. TSK 34. The specimen is housed in the Oxford University Museum.

B. AXIAL SKELETON

1. *Description*

(*a*) *General comments*

Twenty-four presacral vertebrae and the first sacral vertebra were preserved in continuous articulation. Two poorly preserved cervical vertebrae occurred, isolated from the main block and from one another. The possibility remains that other cervical vertebrae were originally present, but otherwise the presacral count (including the atlas and the axis) is 28 (figure 18). This compares with a figure of 27 in *Thrinaxodon* and 29 in *Cynognathus*. Two other sacral-like vertebrae occurred articulated together, but separate from the main block. As the prezygapophyses of the anterior one do not match the postzygapophyses of the first sacral vertebra, at least one and possibly two sacral vertebrae are missing, giving a sacral count of four or five. The normal cynodont number is five. Eighteen caudal vertebrae are present as five short, separate sections and because these sections do not all articulate with one another, there must have been at least several, and possibly many more than 18 tail vertebrae.

The axial skeleton is differentiated into cervical, thoracic and lumbar regions as in later cynodonts, but because the vertebral and rib types grade into one another rather than showing abrupt transitions along the column, it is impossible to give exact numbers of each type.

All of the individual vertebrae are deeply amphicoelous, and there are no intercentra present behind the axis vertebra, with the exception of the caudal vertebrae where intercentral haemal arches are found. The neural arches have not synostosed with the centra, and prominent sutures remain between them. There are nutritive foramina on the lateral surfaces of the centra, which are usually very large. The accessory zygapophyseal articulations (anapophyses) characteristic of the later cynodonts are completely absent in *Procynosuchus*. Similarly, the ribs show no sign of the expanded costal plates which occur in all the typical cynodonts, but are instead of a primitive therapsid nature. On the other hand, the development of short, horizontally orientated ribs, immovably fixed to the transverse processes, occurs in the lumbar region, as in later cynodonts.

(*b*) *The atlas–axis complex*

The right atlas neural arch, the complete axis plus attached atlas centrum, and elements corresponding to a proatlas, an atlas rib and an axis rib are present (figure 1). The whole complex resembles closely that of *Thrinaxodon* and *Galesaurus* (Kemp 1969; Jenkins 1971).

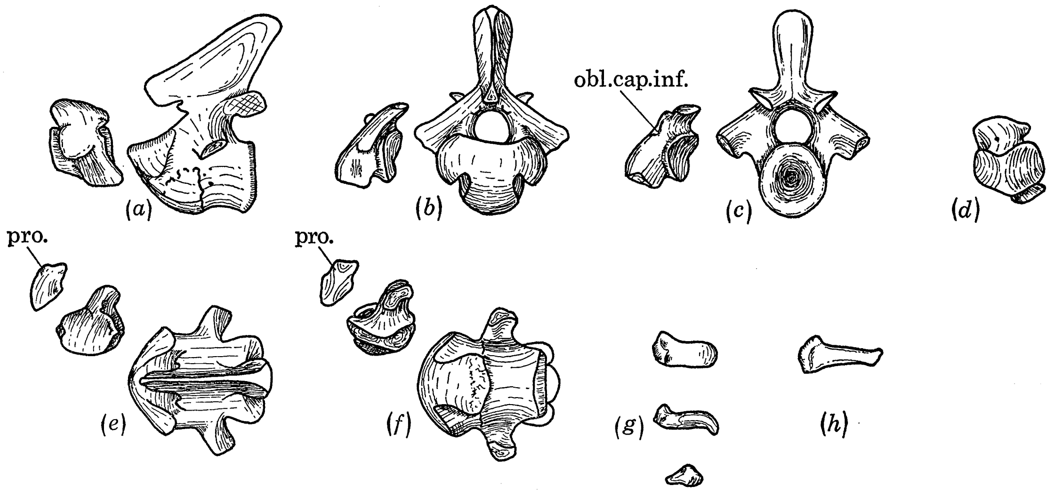

FIGURE 1. Atlas–axis complex. (*a*) Lateral view; (*b*) anterior view; (*c*) posterior view; (*d*) medial view; (*e*) dorsal view; (*f*) ventral view; (*g*) atlas rib in dorsal, posterior and proximal views; (*h*) axis rib in dorsal view. Natural size. Abbreviations: obl. cap. inf., insertion of the obliquus capitis inferior muscle; pro., proatlas.

The principal difference is that the antero-ventral facet of the atlas centrum, which articulated with the posterior face of the atlas intercentrum, is much wider and faces more ventrally. Distinct notches separate this facet from the paired dorso-lateral facets of the atlas centrum for the atlas neural arches. The atlas neural arch bears a small peg-like process on its posterior margin, which probably represents a reduced neural spine by comparison with pelycosaurs (Romer & Price 1940) and dicynodonts (Cox 1959). A ridge, bearing a small tubercle, runs from the process ventro-laterally, part of the way along the posterior edge of the transverse process. The ridge probably indicates the insertion of a muscle from the broadly concave lateral surface of the neural spine of the axis, corresponding to the mammalian obliquus capitis inferior. If so, it would support Cox's (1959) theory that the obliquus capitis inferior muscle was derived from an interspinalis muscle between the atlas and axis neural spines. In *Procynosuchus*, the insertion of the interspinalis muscle on the atlas neural arch has commenced a lateral extension along the transverse process.

The axis vertebra differs from that of the other cynodonts in the shape of its neural spine, which slopes postero-dorsally to overhang extensively the postzygapophyses. The orientation of the postzygapophyses themselves is about 45° from the vertical, in contrast to their almost horizontal orientation in *Thrinaxodon*. The proatlas is perfectly preserved, and is a small, irregularly oval plate. It is curved along its long axis, convex dorsally and concave ventrally. The ventral surface is marked by a longitudinal thickening along the long axis, which ends as a triangular facet, presumably for contact with the atlas neural arch.

The two bones identified respectively as the atlas and the axis ribs occurred in the same block as their respective vertebrae, although separated. The smaller of the two, assumed to be the atlas rib, is only 8 mm long, and 3 mm wide in the centre of the shaft. It is flattened dorso-ventrally and curves slightly downwards towards its distal end. The head arises abruptly from the shaft and is swollen both antero-posteriorly and dorsally. Because of the orientation of the transverse process of the atlas, the rib must have projected ventro-laterally and posteriorly. It is doubtful whether it could have made contact with a parapophysis on the (missing) atlas intercentrum except by connective tissue. The axis rib is similar but larger, with a shaft length of at least 10 mm, and its orientation on the axis was parallel to that of the atlas rib. Comparison of these ribs with those of other cynodonts is not possible for, with the exception of a damaged atlas rib in *Galesaurus*, they are unknown.

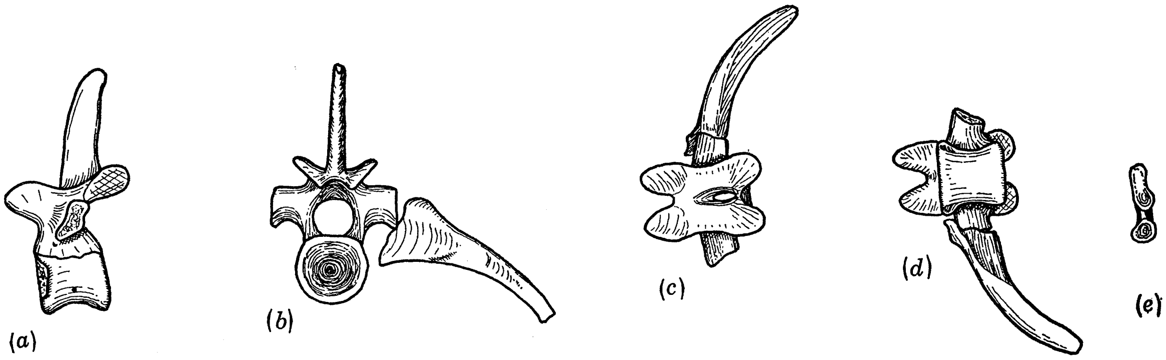

FIGURE 2. Cervical vertebra and rib (vertebra six). (*a*) Lateral view; (*b*) posterior view; (*c*) dorsal view; (*d*) ventral view; (*e*) proximal view of rib head. Natural size.

(*c*) *The presacral vertebrae*

The isolated first two cervical vertebrae are both poorly preserved. The one assumed to be vertebra 3 has a very short, delicate neural spine, which evidently lay below the posteriorly extended neural spine of the axis. The postzygapophyses are widely separated and their articulating surfaces lie at an angle of about 36° to the vertical. The transverse process is distinct from the centrum, and transversely orientated. The vertebra assumed to be 4 has a well preserved neural arch although the centrum is badly damaged. The neural spine is peculiar in that it inclines slightly anteriorly, in contrast to all the succeeding vertebrae. The zygapophyses and transverse processes resemble those of the previous vertebra. The next vertebra, 5 (compare figure 2 with figure 20, plate 1) is the first of the continuous run of vertebrae. Its neural spine is thin and slender, and curves posteriorly. The pre- and postzygapophyses are widely spaced and have an angle of about 33° to the vertical. They are connected on either side by a longitudinal ridge near the base of the neural spine. The transverse process, still distinct from the centrum, runs slightly posteriorly. The relatively small centrum bears a semicircular parapophyseal facet about halfway up its anterior margin. The succeeding vertebrae show a series of morphological gradients towards the structure of the typical thoracic

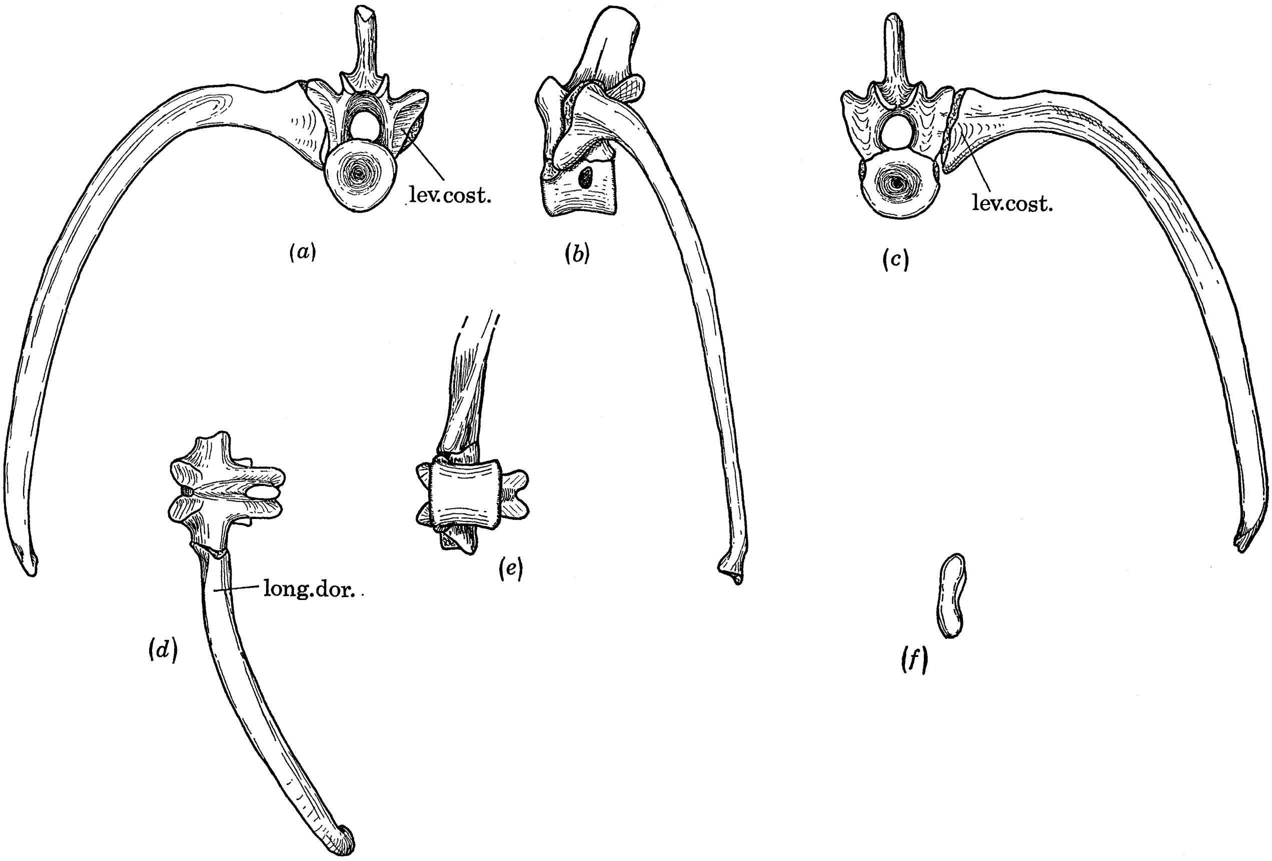

FIGURE 3. Thoracic vertebra and rib (vertebra twelve). (*a*) posterior view; (*b*) lateral view; (*c*) anterior view; (*d*) dorsal view; (*e*) ventral view; (*f*) proximal view of rib head. Natural size. Abbreviations: lev. cost., attachments of the levator costae muscle; long. dor., insertion of the longissimus dorsi muscle.

vertebrae (figure 3). The neural spines become stouter and taller, and lose the posterior curvature, to become straight, tall, but slightly posteriorly inclined. The ridge connecting the pre- and postzygapophyses becomes less prominent and has virtually disappeared by vertebra 10. The transverse process deepens antero-ventrally so that the diapophysis itself becomes deeper, and its ventral end approaches the parapophysis of the centrum. By vertebra 11, the two facets have become confluent, forming a single synapophysis for articulation with the rib. At the same time, the dorsal edge of the transverse process runs dorso-laterally, increasing the height of the synapophysis. The length of the centrum increases slightly. The articulating surfaces of the zygapophyses become more vertically aligned, so that, whereas the anterior zygapophyses of vertebra 8 lie at about 33° to the vertical, by vertebra 12 they form an angle of about 24° to the vertical.

There is, however, no readily definable distinction between cervical and thoracic vertebrae (or ribs, as described below). Vertebra 9 has the prezygapophyses more widely spaced than the postzygapophyses, a reflexion of a change in angle of the zygapophyseal facets from 35° anteriorly to 25° posteriorly. Jenkins (1971) used a similar but more marked change in the seventh vertebra of *Thrinaxodon* as an indicator that seven cervical vertebrae were present. On this argument, *Procynosuchus* has nine cervicals.

From vertebra 10 backwards to about vertebra 16, there is a series of more or less identical, thoracic-type vertebrae (figure 3). The only marked change is a sudden reduction in the height of the neural spine of vertebra 12, compared with those in front (figure 18). The spines of the succeeding vertebrae have broken so it is not possible to tell whether the shorter type of neural spine is continued backwards. From the other dimensions of the spines, it would seem likely. The neural spines of all these thoracic vertebrae slope evenly backwards, and are narrowly oval in cross section. The anterior edge is sharp and, towards the base, the posterior edge is flattened. The prezygapophyses are close together, and their articulating surfaces are trough shaped. The lateral part is close to vertical while the narrow medial part approaches horizontal. The postzygapophyses are correspondingly convex from side to side. Jenkins (1971) has described similar peg-and-socket zygapophyses in at least *Galesaurus*, although they differ in *Procynosuchus* in that the paired prezygapophyses are separated in the midline by a narrow fissure, rather than confluent. The ribs of the thoracic vertebrae articulate with the synapophysis, formed from the deep diapophysis extending antero-ventrally to meet the parapophysis. The dorsal end of the synapophysis lies almost level with the upper edges of the zygapophyses. The facet also runs ventro-medially, so that in anterior view the lower end of the transverse process is seen to reach the lateral face of the centrum. This gives the vertebra a 'skirted' appearance, in contrast to the distinct transverse processes of the cervical vertebrae. There is no extension of the facet for the rib onto the posterior edge of the next anterior centrum, in contrast to the situation in typical cynodonts.

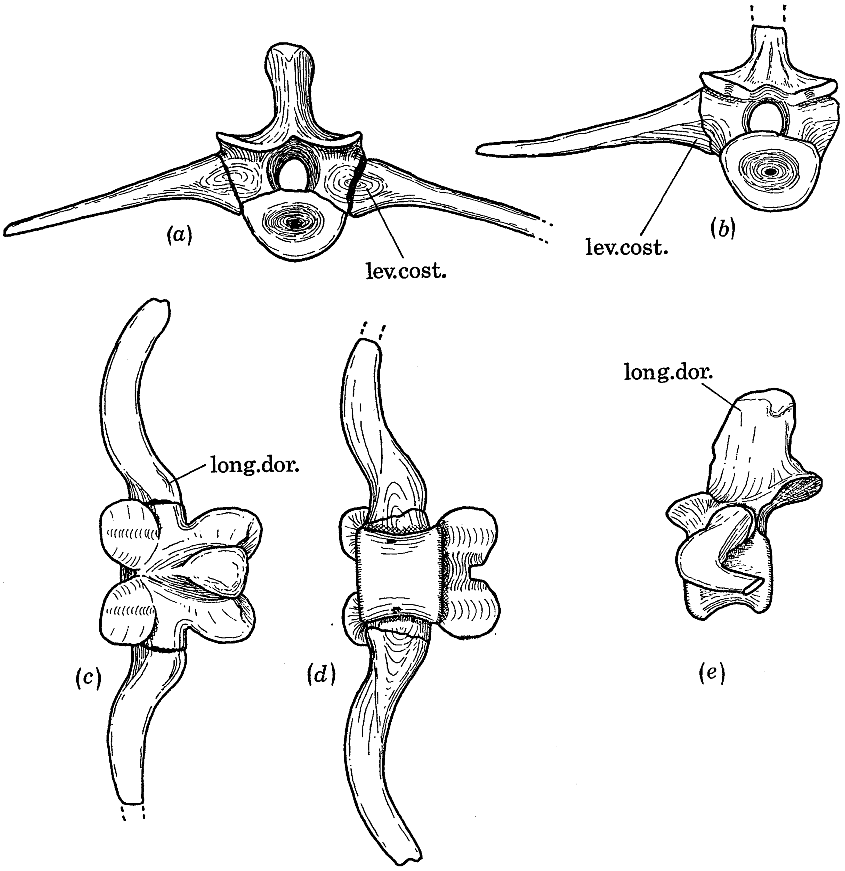

FIGURE 4. Lumbar vertebra and rib (vertebra 26, except (*b*), which is vertebra 25). (*a*) Anterior view; (*b*) posterior view; (*c*) dorsal view; (*d*) ventral view; (*e*) lateral view. Natural size. Abbreviations: lev. cost., attachments of the levator costae muscle; long. dor., attachments of the longissimus dorsi muscle.

From about the 16th vertebra backwards (figure 21, plate 1), there is a gradual transition in form to the lumbar type of vertebrae (figure 4; figure 23, plate 1). Most significantly, the width of the zygapophyses increases, a reflexion in small part of increasing robustness of the vertebrae, but mostly of a gradual change in angle of the zygapophyseal facets. On vertebra 15, the zygapophyseal angle is about 35° to the vertical, by vertebra 20 it is 64° to the vertical, and by vertebra 25 it is 70°, which is virtually horizontal. Coupled with this trend is a gradual increase in the length of the centrum from about 10 to about 11.5 mm, and also an increase in both the antero-posterior length and the transverse thickness of the neural spines. Nevertheless, there is no basis for a rigid separation of the thoracic series from the lumbar series, the transition being gradual. The typical lumbar type of vertebra has a very robust appearance. The neural spine is triangular in section, with a sharp anterior edge but much thickened posterior edge. As indicated, the broad prezygapophyses appear superficially to be almost horizontal, and the articulating surface of each bears a slight longitudinal ridge, about halfway between its lateral and medial edges. This corresponds to a faint longitudinal groove in a corresponding position on each of the postzygapophyseal articulating surfaces. The medialmost part of the prezygapophysis is slightly more horizontal than the rest, and this corresponds to the structure of the thoracic vertebral zygapophyses, noted above.

(*d*) *The presacral ribs*

The first rib actually preserved in articulation with a vertebra is the right one of vertebra 11, and is no more than an incomplete head. However, a series of five disarticulated right ribs lay alongside the anterior vertebrae, and they are interpreted as right ribs 6 to 10 (figure 20, plate 1). On the left side, the first rib in articulation with its vertebra is number 13, but two more or less identical ribs nearby have been assumed to belong to vertebrae 11 and 12. The most delicate of the right ribs (figure 2), interpreted as cervical rib 6, has separate capitular and tubercular facets, which are connected by a thin sheet of bone, forming a triangular head in anterior view. The shaft curves posteriorly and ventrally from the head and is trough-like along its hind face. Although the shaft is broken distally, its thinness indicates that little is missing, giving it a length of something over 25 mm. The next rib, 7, consists only of a fragment of the head, but the succeeding three ribs show a transition towards a larger head, approach of the tubercular facet towards the capitular facet, and a thicker, longer, but still posteroventrally curving shaft characteristic of the later thoracic ribs. The first rib to show confluence of the tuberculum and capitulum is rib 11, which corresponds to the confluence of parapophysis and diapophysis of vertebra 11.

The typical thoracic ribs (figure 3) have a very flat, triangular head. The single, compound articulating surface is a long, narrow strap occupying the full length of the proximal end, and corresponding closely in form to the synapophysis of the vertebra. The rib shaft extends laterally and slightly posteriorly from the head, and then turns quite abruptly to run ventrally as well. The dorsal edge of the proximal part of the shaft is sharp, and distally it becomes the postero-dorsal margin of the shaft. A slight ridge on the anterior face of the head develops distally into the antero-dorsal edge of the shaft. Thus, the dorsal surface of the shaft beyond the bend is relatively broad. The ventral edge is sharper, and running down both the anterior face and the posterior face is a shallow groove. The only absolutely complete thoracic rib is the left twelfth. It shows a gradual attenuation distally. At the distal end the shaft swells slightly to accommodate a ventrally facing, oval facet. No doubt a cartilaginous ventral rib extended the rib shaft medially. Fine longitudinal striations mark the dorsal surface of the rib shaft.

From about rib 16 backwards, there is a gradual transition into lumbar type ribs (figure 18). Rib 16 has the typical bend of the shaft ventrally, but in rib 17, the bend is less pronounced and occurs more distally. By rib 20, which is completely preserved on both sides, there is no abrupt bend at all. Instead, the rib shaft curves continuously from the head, and it runs more posteriorly and less ventrally. The total length of the shaft is about the same as in the thoracic ribs. The dimensions and orientation of the head are also similar, but the dorsal ridge of the proximal end of the shaft extends further distally before rounding off as the postero-dorsal margin of the rib shaft. The trough along the anterior face of the shaft is less prominent. The distal end of this rib has a similar, oval facet for a cartilaginous extension as do the thoracic ribs, but it faces postero-ventrally and medially. From rib 20 backwards, there is a rapid transition of the ribs, with the shaft becoming shorter and more horizontally disposed, although retaining its posterior curvature. The shaft also flattens in the horizontal plane. The articulation facet of the rib becomes shorter but the angle of its attachment to the synapophysis remains about the same. By rib 23, the shaft is virtually horizontal, curves gently posteriorly, and is completely flattened dorso-ventrally. The head also becomes increasingly closely attached to the vertebra. By vertebra 25, there was clearly no longer any possibility of independent movement of the rib. However, the ribs and vertebrae never actually synostose, for a suture is always easily visible. The dorsal ridge of the proximal end of the rib, prominent in all the ribs, becomes even more marked, and coursely rugose, in ribs 22 and 23. From rib 24 backwards, however, the proximal part of the rib expands to form a broad, horizontal face, which is continuous proximally with the dorsal surface of the transverse process, and distally with the dorsal surface of the rest of the rib shaft (figure 4). The posterior edge of the proximal dorsal surface is slightly raised.

The last four lumbar ribs 25–28 (figure 23, plate 1), run slightly anteriorly from the head, before curving back posteriorly. They have of course become very short, the last one barely extending laterally beyond the first sacral rib.

(*e*) *The sacrum*

The first sacral vertebra (figures 5 and 23) is preserved in articulation with the last of the presacrals. Its prezygapophyses are identical to those of the lumbar vertebrae, being very broad, with almost horizontally orientated facets. The postzygapophyses in contrast, are very much smaller, closer together, and have articulating surfaces at about 33° to the vertical. The neural spine lacks the distal part. It is about the same antero-posterior length as the lumbar spines, but rather thinner. The centrum has approximately the same dimensions as the lumbar centra. The rib articulates with a synapophysis of the same structure as in the preceding vertebrae, although the rib head is much thicker. The distal face of the sacral rib faces slightly dorsally as well as laterally, which appears to be natural despite the incongruity with the vertical medial face of the ilium. It suggests that the sacral articulation involved considerable connective tissue. The articulating surface of the rib consists of a broad postero-ventral plate, and a narrower antero-dorsal extension. Both are heavily rugose, as is the dorsal surface of the distal part of the rib shaft.

The only other part of the sacrum present is two vertebrae in close articulation with one another, each with a large, sacral-like rib (figure 5). The prezygapophyses of the more anterior

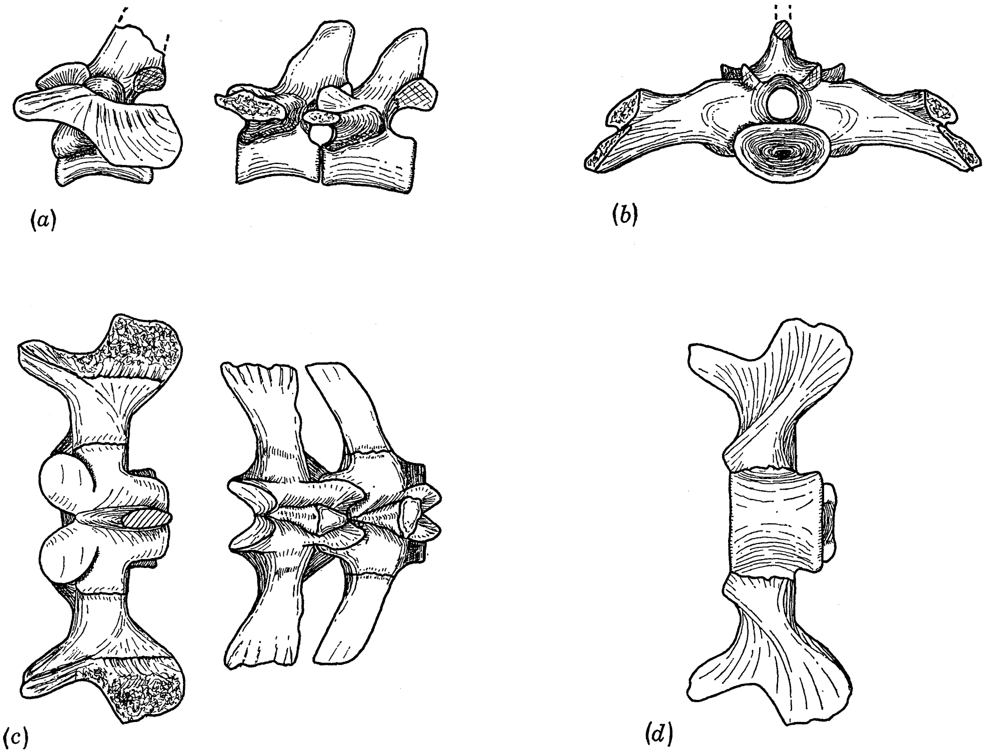

Figure 5. Sacral vertebrae and ribs. (*a*) Lateral view of the first and the last two sacrals; (*b*) posterior view of the first sacral; (*c*) dorsal view of the first and the last two sacrals; (*d*) ventral view of the first sacral. Natural size.

vertebra have some resemblance to thoracic prezygapophyses, being trough-like with a medial part close to horizontal and a lateral part much more vertical. They are too closely spaced to allow articulation with the postzygapophyses of the first sacral vertebra, and it is concluded therefore that at least one sacral vertebra intervened. The length of the ilium is so short that, even with a single extra sacral vertebra, the posterior one would make only a partial contact with the ilium. The neural spines of both of these preserved vertebrae are short and robust. They taper dorsally to a thick, irregular distal end, and the anterior edges of the spines are thick and rugose. The tightly fitting zygapophyses which connect the two vertebrae are of the trough and peg type, and the postzygapophyses of the hinder one indicate that the articulation with the next posterior vertebra was similar. The ribs are fused to the vertebrae, and both are flattened dorso-ventrally and inclined somewhat anteriorly. The anterior of the two ribs is the larger.

(*f*) *The caudal vertebrae*

The eighteen caudal vertebrae preserved occur as five separate blocks. The most anterior block, consisting of one incomplete vertebra and a second complete one behind, is probably from the anteriormost region of the tail, for these vertebrae are not much smaller than the last sacral vertebra. The centrum is greater in width than in length, and is slightly oblique relative to the neural arch, for the posterior part is lower than the anterior part. This presumably relates to the postero-ventral line of the anterior region of the tail. The zygapophyses are relatively widely spaced, and have the peg and trough form found in the thoracic vertebrae. The transverse processes of both vertebrae are missing, but their bases are fairly robust. A fragment of an intercentral element, presumably a haemal arch, lies between the centra.

The next two series of preserved vertebrae are similar, but smaller in all respects (figure 6). Transverse processes, where preserved, are long, but very thin. Haemal arches occur between several of the vertebrae. They are particularly well developed, being wide antero-posteriorly. Each one slopes postero-ventrally, and widens further at the distal end. The neural spines of all these vertebrae are incomplete, but were clearly delicate.

The next series consists of three very poorly preserved vertebrae. They are very much smaller, and are particularly flattened dorso-ventrally.

The final series (figure 6) probably constitutes the actual tip of the tail. It consists of four practically vestigial vertebrae, relatively very elongated and flattened dorso-ventrally. Elongated neural arches and small haemal arches are present.

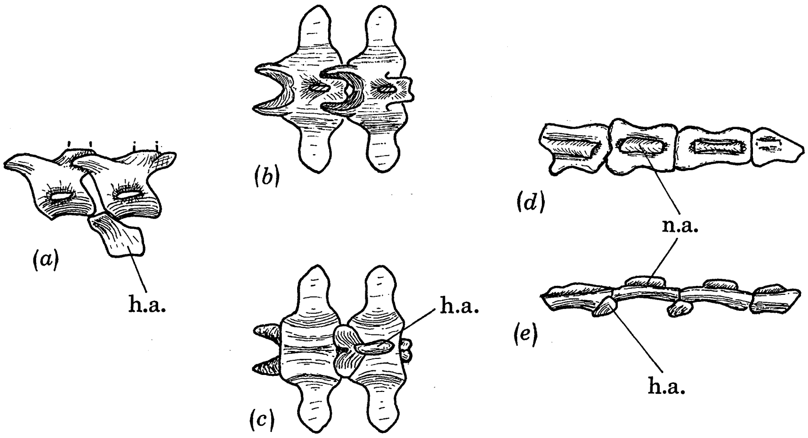

FIGURE 6. Caudal vertebrae. (*a*) Lateral view of two fairly anterior caudals; (*b*) dorsal view of the same; (*c*) ventral view of the same; (*d*) dorsal view of the terminal caudals; (*e*) lateral view of the terminal caudals. Natural size. Abbreviations: h.a., haemal arch; n.a. neural arch.,

2. *Functional interpretation*

(*a*) *Overall form of the axial skeleton*

Determination of the shape of the vertebral column is difficult because the centra had unossified connective tissue separating them. Similarly, the absence of the layers of articular cartilage that must have been present on the zygapophyses prevents a precise analysis of their respective positions relative to one another. The ribs of the dorsal region, however, suggest that a small degree of dorsal arching of the vertebral column occurred (figure 18). A series of the thoracic type of ribs, identical as far as they are preserved, extend from the region of the shoulder girdle to approximately vertebra 18. Further posteriorly, the ribs gradually come to incline more posteriorly. Therefore the distance between their distal ends increases, unless the body axis is assumed to develop a dorsal bow from about vertebra 19 backwards.

The structure of the neural spines of the cervical vertebrae indicates that the neck curved upwards to elevate the head above the level of the shoulder girdle region. The very short spine of cervical vertebra 3 allows the neural spine of the axis to overhang it, and the antero-dorsal inclination of the spine of cervical vertebra 4 permits a relatively large dorsalward bend of the neck between vertebrae 4 and 5. The slender nature of the neural spines of vertebrae 5, 6 and to a lesser extent 7, similarly create sufficient space for an upward bend of the neck in this region.

The rib cage is more extensive than in later cynodonts, due mainly to the presence of long rib shafts in the more anterior lumbar region. There is an abrupt change in the curvature of the ribs between vertebrae 20 and 21. The 20th rib is the more curved and follows the general structure of the previous thoracic ribs. Rib 21, however, although still long, is distinctly less curved. It is possible that this indicates the presence of a mammal-like diaphragm bounding the pleural cavity posteriorly at the level of rib 20, and involved in breathing. A similar suggestion has been made by Brink (1955) with respect to the later cynodonts.

The cross section of the body, as indicated by the more complete of the ribs, is a dorsally flattened circle in the thoracic region. In the anterior lumbar region, the width of the body may have come to exceed the height, giving a dorso-ventrally flattened oval shape.

The tail is much longer and more robust than the reconstructions of *Thrinaxodon* (Jenkins 1971) or *Diademodon* (Brink 1955) indicate for these respective genera. While a well developed tail is undoubtedly primitive, this feature, along with the presence of robust, antero-posteriorly elongated haemal arches, can be correlated with the use of the tail in aquatic locomotion, as discussed later.

(*b*) *Intervertebral movements*

With around 20 vertebrae between the anterior and posterior limb girdles, it requires only a very few degrees of movement between adjacent vertebrae to give a quite large flexibility to the vertebral column as a whole. Therefore it is practically impossible to deny that flexibility in any particular plane could have existed, from a study of even perfectly preserved zygapophyses such as those of the present specimen. On the other hand, the very fact that differences in zygapophyseal orientation do occur in different regions of the vertebral column suggests that these joints are important in promoting some kinds of movements between adjacent vertebrae and restricting others, and therefore a few general observations are permissible.

The peg-and-trough type of zygapophyseal articulation described for the thoracic region, permits ample dorso-ventral rotation of one vertebra on the next. The dorsal movement is soon restricted by the apposition of the respective neural spines, but this restriction is less than in later cynodonts, where each neural spine lies in a groove in the posterior edge of the next anterior spine, the two being very nearly in contact. Lateral bending of adjacent vertebrae is severely limited in the thoracic region, for the lateral facing surfaces of the postzygapophyses lock against the medial-facing surfaces of the prezygapophyses almost instantly, even in the absence of layers of articular cartilage which would make the fit tighter still. On the other hand, this design of zygapophyses permits relatively easy rotation of one vertebra relative to the next, about a longitudinal axis. The axis of this form of rotation lies dorsal to the level of the zygapophyseal articulating surfaces, and therefore such movement tends to cause a lateral shift of the centrum of one vertebra relative to the next. Since only a very small shearing movement between the centra would be likely, the amount of rotation of adjacent vertebrae must have been small. Nevertheless, the possibility of a twisting of the vertebral column as a whole remains a conceivable part of the locomotory mechanism.

The large, flat, near-horizontal zygapophyses of the lumbar region are, perhaps, the most unexpected anatomical feature of *Procynosuchus* to emerge in this study. They permit a very large lateral rotation of adjacent vertebrae. The reduced lateral extent of the ribs of the lumbar region reduces the tendency for the ribs to limit lateral flexion. Furthermore, these lumbar ribs appear to have been capable of riding over one another. Certainly this is true of the ribs of vertebrae 23 to 28, where the ribs become very short, and practically horizontal in orientation. It is not clear whether the more anterior rib would have passed dorsal or ventral to the more posterior rib. The transition from the near-vertical thoracic type of zygapophyses to the near-horizontal lumbar type occurs gradually between approximately vertebrae 19 to 23. The amount of total lateral rotation between vertebra 20 and the sacrum could easily have been adequate to create an arc of 90°. In contrast, the lumbar type zygapophyses prohibit rotation about a longitudinal axis more or less completely. Dorso-ventral flexion movements cause an immediate loss of contact of the prezygapophyses from the postzygapophyses except at one point. Thus, although the zygapophyses do not physically prevent this kind of movement, they indicate that it was not a normal part of the animal's activity.

The zygapophyses of the cervical vertebrae are less well preserved. They appear to resemble the thoracic zygapophyses in general, but are less close to vertical, and their articulation faces are flat rather than trough-and-peg shaped. They would appear to have permitted fairly free dorso-ventral flexion and lateral movements, but to have restricted rotation about a longitudinal axis.

The special case of movements of the atlas–axis complex has been discussed at length with respect to galesaurid cynodonts (Kemp 1969). The structure of these bones of *Procynosuchus* are sufficiently similar to those of the later forms that the conclusions presented then apply equally here. The joint between the occipital condyles and the atlas neural arches permits free dorso-ventral flexion–extension movements. Rotation about a longitudinal axis is a function shared by both this joint and that between the atlas elements and the odontoid fused to the axis.

(*c*) *Rib function*

The ribs of the whole of the dorsal region are attached very strongly to the vertebrae by the confluent capitulum and tuberculum facets articulating with a synapophysis, formed from the diapophysis and parapophysis. The explanation for this extensive articulation is probably that the thoracic ribs had an important function mechanically, namely that of resisting lateral movements of the vertebrae relative to one another. Moveably articulated ribs, as thoracic ribs must be to retain their respiratory function, cannot be used to preserve the rigidity of the vertebral column unless they themselves can be held rigid relative to the vertebrae to which they are respectively attached. Therefore, well developed muscles would be necessary, attaching to the rib and running both anteriorly and posteriorly, to attach to the vertebral column. Evidence for such muscles is presented below. Furthermore, the joint between the rib and its vertebra must be strong enough to withstand the forces of these muscles and not suffer disarticulation. The synapophyseal arrangement appears to satisfy this requirement.

The ribs of the lumbar region also attach by a synapophysis, but increasingly they tend to become immovably fixed to the vertebrae, until by about vertebra 24 no movement at all appears to have been possible. In this region, where extreme lateral flexibility has already been demonstrated, the ribs acted as levers assisting the movements of the vertebrae. As indicated, they are much shortened, nearly horizontal, and could overlap one another, all of which subserve their function as levers, acting in the horizontal plane.

(*d*) *Axial musculature*

Jenkins (1971) has reviewed the epaxial musculature of modern reptiles and mammals, and has attempted a reconstruction of these muscles in *Thrinaxodon*. This, however, was with particular reference to the problem of the expanded ribs in the later cynodonts. *Procynosuchus* shows no evidence of a highly specialized epaxial musculature apart from two points. The levator costae series appear to have been well developed. The origin from the posterior face of the transverse process is indicated by a marked, slightly rugose concavity, and similarly there is a well indicated insertion in the form of the concave area occupying most of the anterior, triangular face of the ribs (figures 3 and 4). Secondly, there is indication of a very well developed longissimus dorsi musculature. The sharp, dorsal margin of the medial part of each rib indicates the insertion of this muscle. In the lumbar region, these ridges are even more prominent, and on vertebrae 21–23 are rugose. However, on the remaining vertebrae, 24–28, the ridge is almost absent, and is represented only by a slightly raised posterior edge (figure 4). In mammals, this muscle gains an origin from the top of the neural spines, and the same may have occurred in *Procynosuchus*, thus explaining the development of the much thicker type of neural spines with bulbous heads, that are found in the lumbar region.

In the thoracic region, the levator costae and longissimus dorsi muscles, acting together, would tend to hold the rib rigidly to its vertebra, therefore permitting the ribs to be used to restrict lateral movements of the vertebral column in this region. In the lumbar region, the same muscles used independently would tend to cause the much shortened ribs to act as levers promoting lateral flexibility. As noted, this functional differentiation of the thoracic from the lumbar regions is directly related to the movability of the thoracic ribs, compared to the immovability of the lumbar ribs.

C. The pectoral girdle and forelimb

1. *Description*

(*a*) *The scapulo-coracoid*

The right scapulo-coracoid is preserved (figure 7; figure 28, plate 2), although the ventral margin is damaged. A perfect left coracoid, along with part of the procoracoid is also present. The scapulo-coracoid differs from other known cynodonts in several respects, some quite fundamental, and this is particularly true of the scapula blade.

The scapula is almost parallel-sided and lacks the narrowing of the base found in *Thrinaxodon* and, even more markedly, in later cynodonts. It curves medially in typical fashion, and also the blade twists about its long axis, so that if the dorsal margin lies parallel to the midline of the animal, the ventral part of the scapula and the coracoid plate are orientated antero-medially at about 30° to the sagittal plane. This twist is characteristic of *Thrinaxodon*, but is apparently absent in the later forms. In marked contrast to all other known cynodonts, the lateral surface of the scapula blade is flat, lacking the lateral reflexion of the anterior and posterior edges, and therefore without a concave spinatus fossa. A slight vertical ridge divides the lateral scapula surface into a faint anterior fossa and a larger but equally faint posterior fossa. The latter is itself divided, by a flattening of the bone, into dorsal and ventral parts. The antero-ventral part of the scapula is in the form of a broad concavity, formed from the abrupt medial inturning of the anterior edge of the bone in the acromion region.

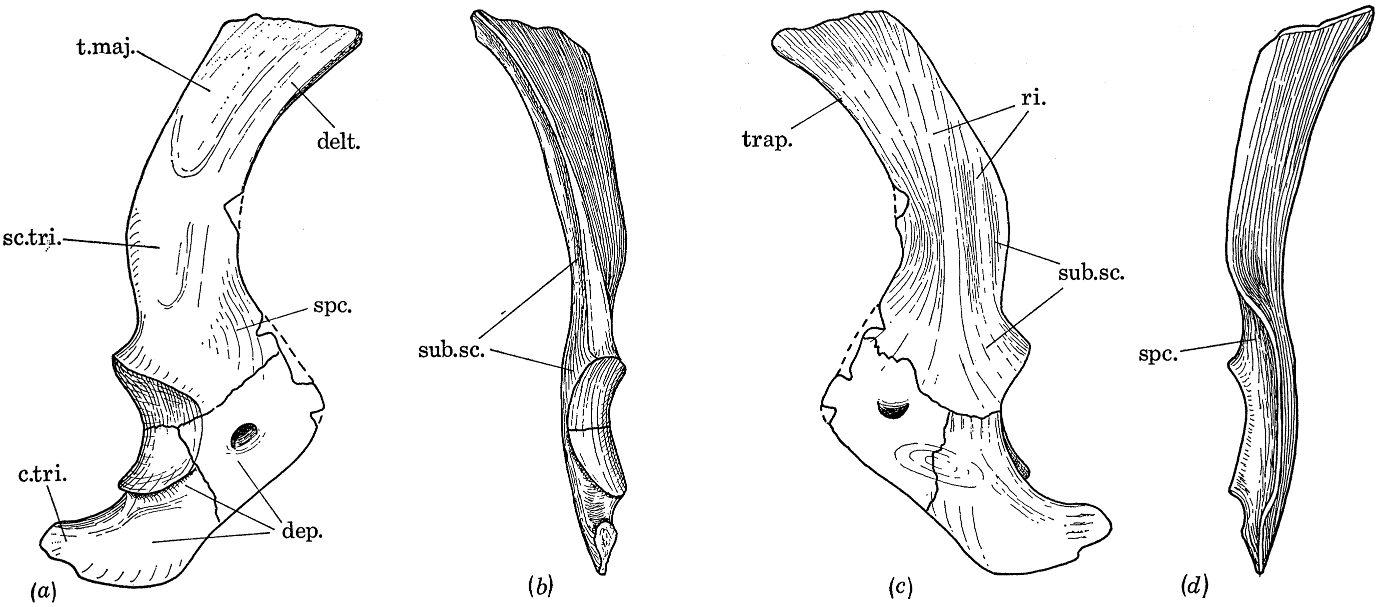

FIGURE 7. Scapulo-coracoid (composite, drawn as the right). (*a*) Lateral view; (*b*) posterior view; (*c*) medial view; (*d*) anterior view. Natural size. Abbreviations: c. tri., coracoid head of the triceps origin; delt., origin of the deltoideus; dep., depression; ri., ridges; sc. tri., origin of the scapula head of the triceps; spc., origin of the supracoracoideus; sub. sc., origin of the subcoraco-scapularis; t. maj., origin of the teres major; trap., insertion of the trapezius.

The medial surface of the scapula also differs radically from that of other cynodonts. A powerful vertical ridge separates a posterior fossa from the broader anterior area. The posterior fossa is further divided by a second, much less prominent vertical ridge into a narrow posterior groove, and a larger anterior groove which commences about one-third of the way down the posterior edge of the scapula, and terminates ventrally as the smooth, convex bone forming the inner surface of the glenoid region. The surface of the scapula anterior to the main vertical ridge consists of a broad, very slightly concave, dorsal area, and a prominent ventral concavity. A slight vertical groove occupies the anterior margin, about one-third of the distance from the dorsal scapula edge.

The dorsal edge of the scapula is straight and poorly ossified, which suggests that in life it was continued by a cartilaginous suprascapula. The anterior edge is rounded over the dorsal half and then becomes very thin and sharp where it curves abruptly medially before meeting the procoracoid. There is no sign of a morphologically distinct acromion process, although the edge of the bone is slightly damaged. The posterior edge of the scapula thickens towards its ventral end, forming a relatively broad, postero-dorsally facing surface above the glenoid.

The coracoid plate is much more similar to that of the other cynodonts than is the scapula. The dorsal margin of the coracoid behind the glenoid, is a fairly broad shelf which faces dorsally and slightly laterally. The medial margin of the shelf is quite sharp, particularly towards its posterior end. This contrasts with the standard cynodont condition, where the medial and dorsal surfaces of the coracoid show a gradual transition. The tuberosity of the distal end of the shelf is flattened latero-medially. The lateral face of the coracoid has three depressions, only two of which are reported in other cynodonts. The largest occupies much of the postero-ventral area, and is completed ventrally by a slight lateral reflexion of the bone. The second occupies the anterior part of the coracoid, and extends onto the procoracoid.

The third, apparently absent in later forms, is a horizontal trough, immediately below the edge of the glenoid. The medial face of the coracoid is gently concave from top to bottom. Fine longitudinal striations mark the posterior part of the surface, and a similar series of vertical striations lie adjacent to the suture of the coracoid with the medial face of the scapula.

The procoracoid has a typical procoracoid foramen, anterior to which the bone is very thin.

The principal difference between the glenoid fossa of *Procynosuchus* and those of later cynodonts lies in the form of the dorsal, scapula part. It faces postero-laterally and ventrally instead of more or less ventrally, and its surface is convex from the medial to the lateral edges, and concave dorso-ventrally. In other cynodonts it is approximately flat, with a concave central area. The ventral, coracoid part is similar to that of other forms. Like the scapula part, it is latero-medially convex and dorso-ventrally concave. The two parts of the glenoid together form a wide, more open fossa, and are smoothly confluent. The glenoid surface faces both more posteriorly, and curves round to face more laterally, than in *Thrinaxodon*. Clearly, as discussed later, the shoulder joint was much less restrictive than in typical cynodonts.

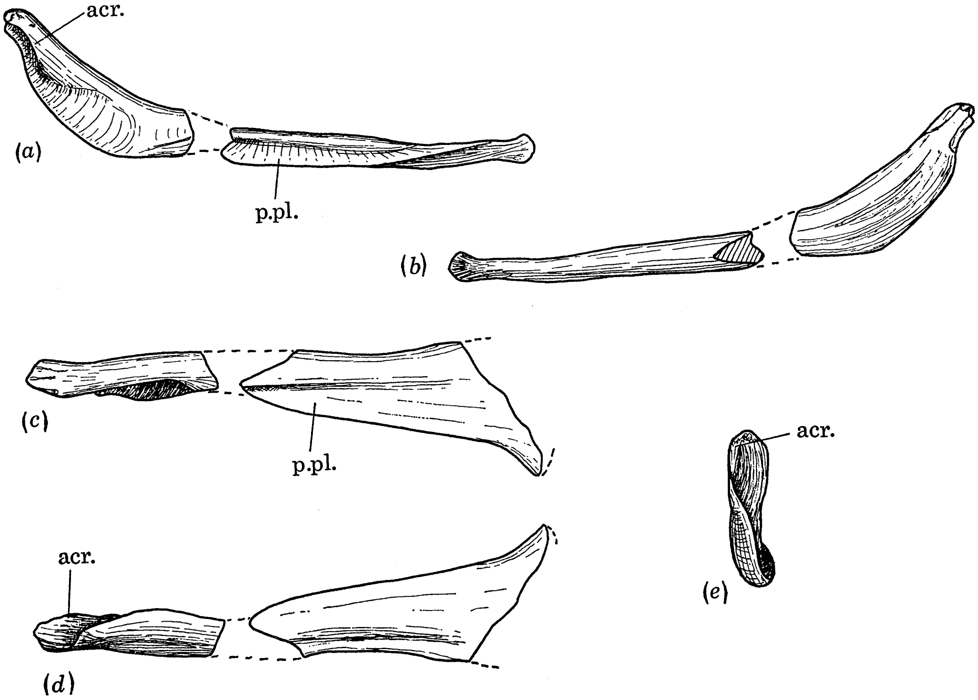

FIGURE 8. Clavicle (composite, drawn as the left). (*a*) Posterior view; (*b*) anterior view; (*c*) dorsal view; (*d*) ventral view; (*e*) lateral view of distal end. Natural size. Abbreviations: acr., postero-dorsal ridge attaching to acromion; p. pl., posterior plate.

(*b*) *The dermal shoulder girdle*

The perfectly preserved lateral end and a large fragment of the medial part of the left clavicle, along with much of the middle region of the right clavicle, are preserved. Together, they permit a reconstruction of the bone lacking only a short segment of the shaft and the extreme medial end (figure 8).

The clavicle is basically like that of *Cynognathus* with its dorsally reflected, spoon-like distal end, and expanded horizontal medial end. The posterior edge of the main part of the shaft is produced posteriorly as a thin, extensive plate.

Of the interclavicle, only a fragment remains. It indicates that the bone was robust, and had the characteristic mid-ventral ridge well developed.

(*c*) *The humerus*

Only the right humerus is present (figure 9; figure 28, plate 2), but is very well preserved. While broadly similar to the standard cynodont pattern, the humerus possesses one marked difference. The delto-pectoral crest is less deflected ventrally from the mainshaft of the bone. It forms an angle of about 145° to the proximal dorsal surface, in contrast to 135°, and usually much less, in other forms. In consequence, the proximal end of the humerus gives the impression of being much broader, and its ventral face is less concave between the anterior and posterior edges. A further difference is that the proximal dorsal surface of the shaft is perfectly flat, in contrast to the more rounded surface of other cynodonts, particularly those later than

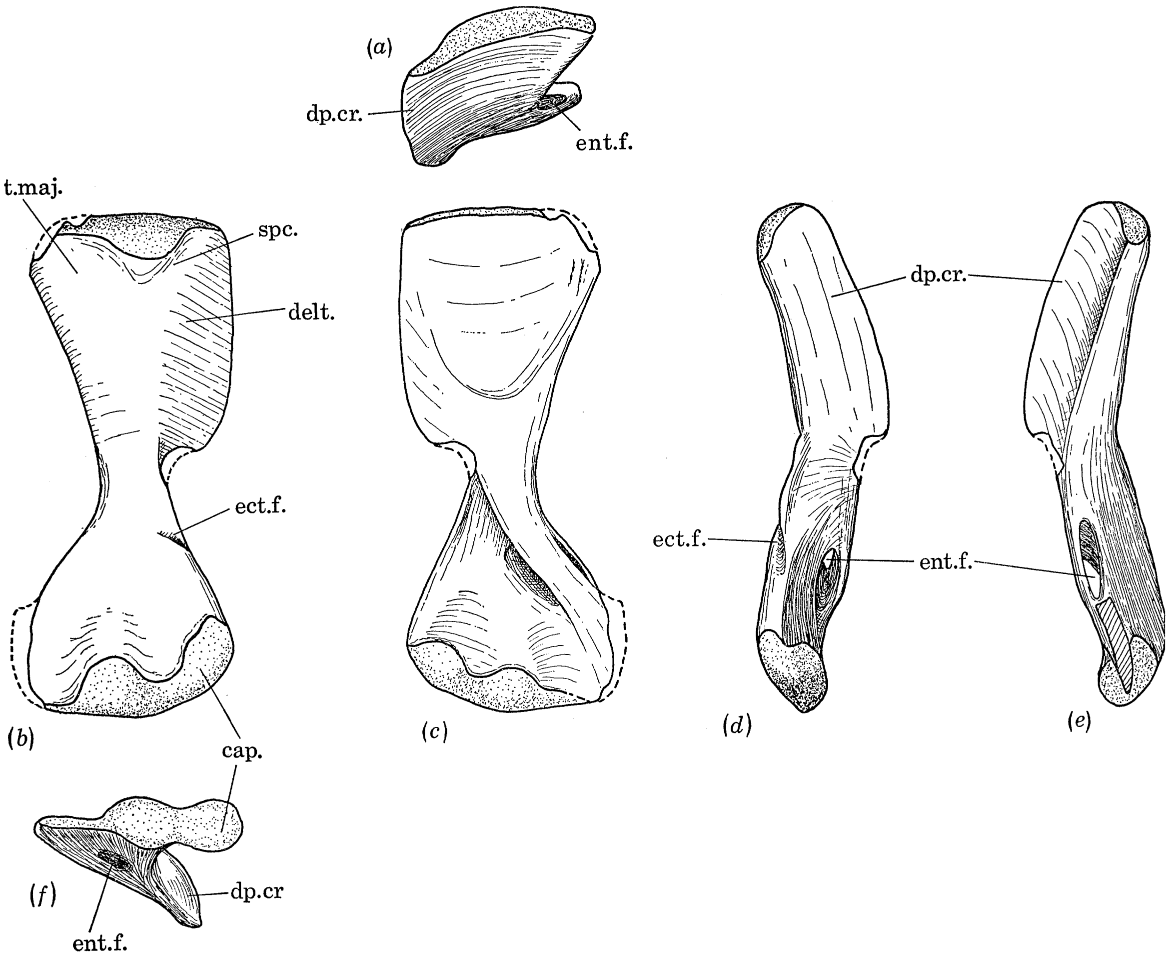

Figure 9. Humerus (right). (*a*) Proximal view; (*b*) dorsal view; (*c*) ventral view; (*d*) anterior (lateral) view (*e*) posterior (medial) view; (*f*) distal view. Natural size. Abbreviations: cap., capitulum; delt., insertion of the deltoideus; dp. cr., delto-pectoral crest; ect. f., ectepicondyle foramen; ent. f., entepicondyle foramen; spc., insertion of the supracoracoideus; t.maj., insertion of the teres major.

Thrinaxodon. The angulation between the proximal and distal parts of the bone is also less in *Procynosuchus*.

The articulating surface of the head of the humerus extends onto the dorsal surface as in other cynodonts, but remains almost flush with that surface, rather than being produced dorsally as a distinctive bulbous head. Jenkins (1971) argues that the head of the humerus of cynodonts was always produced dorsally by cartilage, but at least in this case the shaft immediately distal to the articulating surface shows no sign of having supported a substantially larger cartilaginous head.

The distal half of the humerus is also very flat. Although present, the characteristic depression on the dorsal surface proximal to the trochlea, and on the ventral surface proximal to the capitulum and entepicondyle, are less prominent. Because of the wider dorsal surface of the humerus at the level of the epicondylar foramina, the entepicondyle foramen is not visible in dorsal view, as it is in other cynodonts.

The ectepicondyle foramen is represented by a groove, because of slight damage, and the entepicondyle is also damaged.

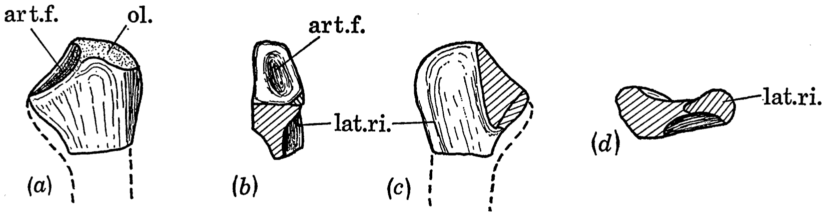

FIGURE 10. Ulna (proximal end of the right). (*a*) Posterior view; (*b*) medial view; (*c*) anterior view; (*d*) ventral view. Natural size. Abbreviations: art. f., articulation facet for the humerus; lat. ri., lateral ridge; ol., olecranon process.

(*d*) *The radius and ulna*

Only a very poorly preserved fragment of what is probably the proximal end of a radius is present. All that can be said is that the shaft is flattened. One face is concave from side to side, and the opposite face is correspondingly convex. One of the edges between these two faces bears a deep vertical recess.

Of the ulnae, again only the damaged proximal end of the right one is preserved (figure 10). The facet for articulation with the humerus is set at about 45° to the line of the shaft, and is in the form of a narrow, fairly deep groove. A low, incompletely ossified olecranon process is present. The shaft itself is extremely flattened but is strengthened by a substantial ridge down its lateral edge.

(*e*) *The manus*

The right manus (figure 11; figures 26 and 27 plate 2) is well preserved, but lacks metacarpals I and V, and all of the phalanges. The full reptilian complement of eleven ossicles form the carpus, there being five distal carpals as well as two centrales, radiale, intermedium, ulnare and pisiform. They lie in an approximately correct relation to one another. The intermedium and proximal centrale are virtually fused, as in mammals. The manus is the least understood part of the cynodont skeleton (Jenkins 1971) and is therefore described in detail.

The ulnare is very flat, and the anterior, lateral and posterior edges are thin. However, the bone thickens medially, and forms a prominent medial shelf underlying the proximal centrale,

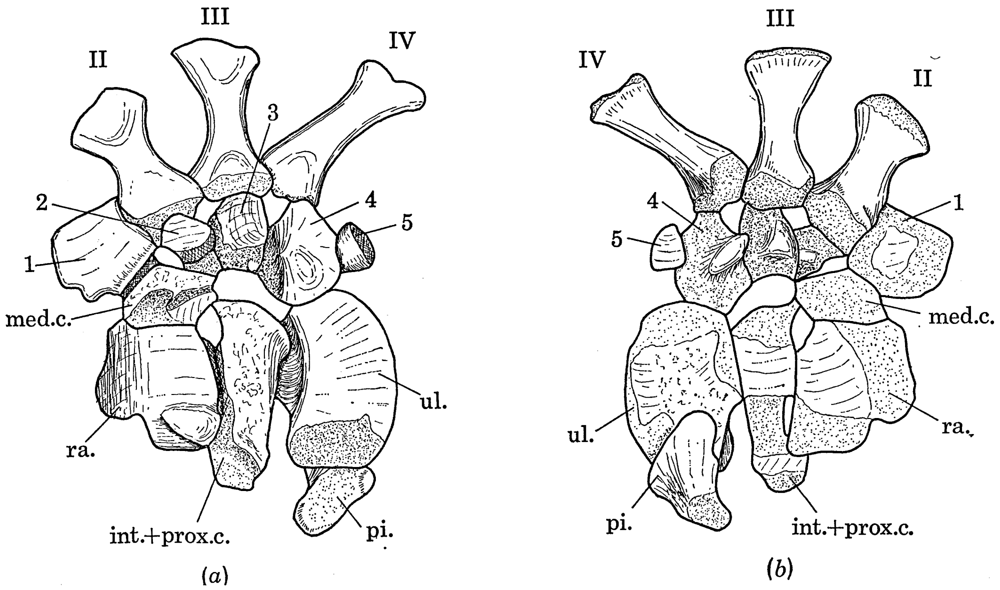

FIGURE 11. Manus (right), as preserved. Incompletely ossified surfaces stippled. (*a*) Dorsal view; (*b*) ventral (plantar) view. (Magn. × 1.5.) Abbreviations: int. + prox. c., intermedium plus proximal centrale; med.c., medial centrale; pi., pisiform; ra., radiale; ul., ulnare; 1 to 5, distal carpals; II to IV, metacarpals.

a feature not reported previously in cynodonts. The dorsal surface of the ulnare is flat, except for a poorly ossified oval concavity posteriorly, for reception of the ulna. Very fine striations radiate laterally from a point halfway along the medial edge. The ventral surface is rugose and is incompletely ossified in the anterior and posterior parts.

The pisiform is preserved partly beneath the ulnare, and is irregularly triangular with a narrow posterior boss.

The intermedium and proximal centrale together effectively form a single elongated bone, with the anterior half supported ventrally by the shelf of the ulnare. The lateral contact, with the radiale, is by a vertical face. The convex anterior face must have contacted distal carpals 2 and 3 in life, again by simple buttresses. Both the dorsal and the ventral surfaces of the complex are rugose. A poorly ossified irregular boss occupies the posteriormost region.

The radiale is the thickest bone of the carpus, and the respective faces for contact with the intermedium–proximal centrale laterally, and the medial centrale anteriorly, are broad and vertical, suggesting that little movement took place. The dorsal surface is convex from side to side and curves smoothly round to the medial face. There is no specifically defined facet for the radius. Of the ventral surface, only the central area has a periosteal layer, and is concave and rugose.

The medial centrale is thinner than the radiale. It bears two prominent grooves on its dorsal surface. The ventral surface lacks a periosteal layer. All of the edges are vertical and, in contrast to Broom's (1948) account of '*Leavachia*', and Bonaparte's (1963) of *Exaeretodon*, the medial centrale must have contacted the proximal centrale, as well as distal carpals 1 and 2.

Of the carpals, the first is the largest and is the characteristically flat, five-sided plate found in other cynodonts. The postero-lateral edge, in contact with the medial centrale, has a slight dorsal lip. Distally, carpal 1 contacted both metacarpals I and II. Carpal 2 is small and its edges are poorly ossified. Carpal 3 has a saddle-shaped dorsal surface, and a small boss on its ventral surface. The large carpal 4 also possesses a saddle-shaped dorsal surface, and a very large ventral boss. The medial face of this carpal is extended as a shelf underlying carpal 3, similar to, and in line with the shelf of the ulnare for the proximal centrale. Carpal 5 is a very small, flat ossicle, preserved partly underlying carpal 4.

Only metacarpals II, III and IV remain. All are flattened dorso-ventrally, although they thicken posteriorly to form poorly ossified articulating surfaces. Ventrally, the posterior ends bear tubercles for the flexor musculature.

The overall flatness of the manus, particularly the metacarpals, suggests that it was adapted for aquatic locomotion. The superposition of the proximal centrale on the ulnare, and carpal 3 on carpal 4, may have strengthened the manus, in relation to its use as a paddle.

2. *Functional interpretation*

(*a*) *Orientation and mobility of the shoulder girdle*

It is, of course, impossible to be sure of the position or range of positions of the shoulder girdle relative to the rest of the skeleton. However, if it is assumed that the flat, dorsal area of the inner scapula surface lay against the rib cage to which it was attached by serratus muscles, then the scapula blade only slopes forwards a relatively small amount, about 20° from the vertical. The twist in the scapula blade causes the coracoid plate to slope antero-medially at about 30° to the midline, and the ventral edge of this plate runs antero-dorsally fairly steeply, at some 35° to the horizontal (figure 18). Whatever mobility the shoulder girdle may have had, this at least seems to be a reasonable 'resting' orientation. In such a position, the glenoid fossa faces postero-laterally with the dorsal and ventral tips of the fossa approximately one above the other. This contrasts slightly with Jenkins's (1971) reconstruction of the shoulder girdle of *Thrinaxodon*, where the dorsal tip is a little posterior to the ventral tip. The latero-medial convexity of the articulating surface extends through almost 90°, so that while the posteriormost part faces posteriorly, the anteriormost part faces exactly laterally. The incompleteness of the clavicles and interclavicle of this specimen does not permit the use of these bones to confirm this proposed orientation.

At any event, scapulo-coracoid mobility was undoubtedly a feature of the shoulder girdle. It is a normal feature of most modern mammals (Jenkins 1974) and lizards (Bellairs 1969), and without it, the forelimb does not appear to have been capable of as great a stride length as the hindlimb, an impossible situation. Indeed, the length of stride possible using the forelimb mechanism proposed by Jenkins (1971, figure 42), for cynodonts in general is extremely short, being about 12 % of the presacral length if possible shoulder girdle mobility is ignored.† The acromio-clavicular joint of *Procynosuchus*, as of other cynodonts, is peculiar in that the large lateral end of the clavicle is associated with an acromion so thin that it is broken off, leaving only a very thin margin of bone. The lateral end of the clavicle bears a postero-dorsal ridge (figure 8), the lower margin of which approximately follows the line of the anterior edge of the acromion region of the scapula. This suggests that the connection was ligamentous and hinge-like and that the scapulo-coracoid could rotate about the clavicle. Such a movement would cause the glenoid to face more anteriorly or more posteriorly, and could thus impart

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† Jenkins's (1971) reconstruction of the complete skeleton of *Thrinaxodon*, given as his frontispiece, should be treated cautiously, for the drawing of the vertebral column appears to have been given a greater reduction (*ca.* × 0·7) than the drawing of the limbs and girdles (*ca.* × 1.0). Thus, the limbs appear to be disproportionately large.

to the humerus a greater protraction–retraction, relative to the ground. A second possible movement could occur by the horizontally flattened, medial end of the clavicle rotating in a horizontal plane upon the flat facet of the interclavicle which receives it. The effect would approximate to an anterior–posterior movement of the scapulo-coracoid, analogous to one of the modes of movement of the scapula of certain modern mammals (Jenkins 1974). This too would effectively increase the overall stride length of the forelimb.

(*b*) *Orientation and movement of the humerus*

The shoulder joint of cynodonts is one of the most problematical regions of all to interpret because of the extreme incongruity of the glenoid and humerus articulating surface. In life, cartilage may have made them somewhat more compatible, but an absurdly thick layer would be required to achieve complete congruity, and there would remain no obvious explanation for the fact that the bony surfaces were so different from the cartilaginous surfaces covering them.

The glenoid of *Procynosuchus* is essentially saddle-shaped. It is concave in a dorso-ventral direction. From the medial to lateral edges, however, it is convex, both the scapula part above and the coracoid part below curving smoothly round from posterior to lateral through about 90°. Unlike other cynodonts, the two respective parts are very similar to one another, creating a symmetry about a horizontal line. The articulating surface of the head of the humerus is strongly convex dorso-ventrally, and the middle part of the surface extends right round on to the dorsal surface. Antero-posteriorly, the articulation is almost linear. Jenkins (1971) suggested that the scapula and coracoid parts of the cynodont glenoid represented a functional division, analogous to the division of the pelycosaurian glenoid into two parts, anterior and posterior. However, the reorientation and widening of the cynodont glenoid allowed a greater degree of freedom to the humerus than could occur in the primitive group. He proposed that the ventral, coracoid part of the glenoid functioned during the recovery phase, with the distal end of the humerus elevated and the proximal end depressed (and added the unlikely suggestion that the reason why the convexity of the coracoid facet reduced contact between the humerus and the glenoid to a point, was to minimize friction). The dorsal, scapula part of the glenoid functioned during the power stroke, the distal end of the humerus being depressed and the proximal end raised. The scapula then received the antero-dorsally and somewhat medially directed propulsive thrust.

Jenkins's hypothesis fails to account for several features of the shoulder joint, most notably why a ball-and-socket joint had not evolved, which would appear to have been a far more satisfactory type of joint to perform the required movements. It also leaves unexplained the fact that the glenoid is widely open posteriorly, when some kind of posterior buttress would be essential if posteriorly directed retractor muscles were to be used to provide part of the power stroke. Thirdly, the proposed rotation of the humerus so that the head goes up when the distal end is depressed, and vice versa, demands a complex muscle arrangement. The moment produced by the muscles would have to act about a fulcrum distal to the articulation, rather than at the articulation itself. It is difficult to conceive of an appropriate muscle arrangement in cynodonts.

There is a sequence of movements of the humerus in the glenoid in *Procynosuchus*, which both utilizes the whole of the respective articulatory surfaces, and which would be appropriate to a locomotory cycle (figure 12). At the start of the power stroke, the anterior half of the

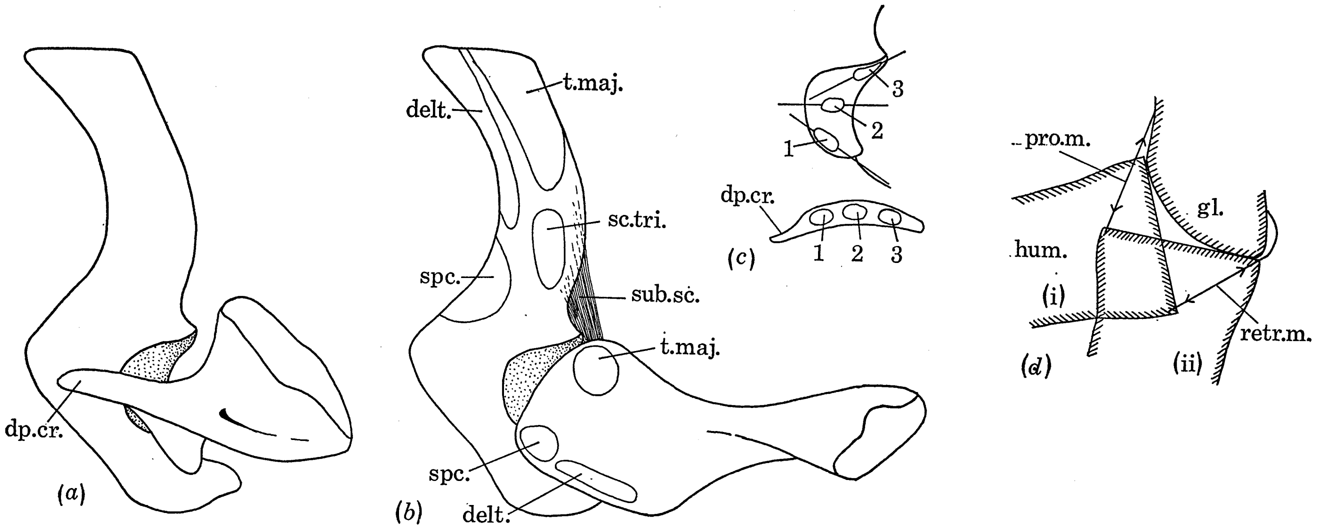

FIGURE 12. Function of the shoulder joint. (*a*) Lateral view of the humerus in the protracted position. (*b*) The same in the retracted position. Note the rotation of the humerus about its long axis, in addition to the retraction. (*c*) Lateral view of the glenoid and proximal view of the head of the humerus, to show successive areas of contact from 1–1 to 3–3. Straight lines represent the orientation of the humerus head at each position. (*d*) Hypothetical horizontal section through the glenoid and humerus, to illustrate the principle of the shoulder joint mechanism. Note that during retraction of the humerus from (i) to (ii), the retractor muscle acts continuously, even though originating from the scapulo-coracoid. Similiarly, during protraction from (ii) to (i), the protractor muscle acts continuously. The apparently extreme degree of muscle contraction in both cases is an artefact arising from ignoring vertical directions. Abbreviations: delt., attachment of the deltoideus muscle; dp.cr., delto-pectoral crest; gl., glenoid; hum., humerus; pro.m., protractor muscle; retr.m., retractor muscle; sc.tri., origin of the scapula head of the triceps; spc., attachment of the supracoracoideus muscle; sub.sc., subcoraco-scapularis muscle; t.maj., attachment of the teres major muscle.

humerus articulating surface lies in contact with the lateral region of the coracoid glenoid, and is aligned antero-dorsally (figure 12*a*, *c*). The shaft of the humerus extends approximately laterally and the distal end faces antero-ventrally. The humerus is retracted, and at the same time rotates about its long axis. The head does not slide across the glenoid surface, but rolls across it (as a wheel over the ground). At first it contacts increasingly posterior and medial parts of the coracoid glenoid, but eventually the dorsal part of the head contacts the lateral part of the scapula glenoid. The final stages of the movement see the humerus head now rolling towards the more posterior and dorsal region of the scapula glenoid (figure 12*c*). During this movement, the degree of long axis rotation is high (up to 90°), and the retraction takes the humerus from laterally orientated to almost posteriorly orientated (figure 12*b*). At any point in the stride, there is a considerable freedom of adduction–abduction, so that the distal end of the humerus may be elevated or depressed. Because of this, the recovery stroke can be a retracing of the same course of the humerus head over the glenoid, but with the humerus held in an abducted, elevated position. Not only does this proposed movement involve virtually the whole of the glenoid and humeral articulatory surfaces, it also suggests certain explanations for the geometry of the joint surfaces.

Theoretically, the same movements could be achieved by a ball-and-socket joint, with the added advantage that a large surface area of contact between the glenoid and the humerus articulation could be maintained, giving a more stable, stronger joint. However, the fact that the glenoid surface is convex in the horizontal plane (i.e. convex with respect to the protraction–retraction component of humerus movement), while the humerus head has a linear articulating surface, has two implications (figure 12*d*). The first is that the effective fulcrum of the humerus rotation in the horizontal plane lies a little more proximal than the head. Thus the humerus is effectively longer and the stride greater. A second, and probably even more important consequence, is that by use of the rolling movement of humerus head over the glenoid, a large amplitude of humeral retraction–protraction is possible without the anterior or posterior ends of the humerus head passing medial to the levels of the anterior or posterior margins of the glenoid fossa. Muscles attaching to the anterior and posterior corners of the humerus respectively, can attach exclusively to the scapulo-coracoid. They will produce respectively protraction and retraction movements of the humerus over the whole range of humerus movement (figure 12*d*). If a ball-and-socket type of shoulder joint were present, then the posterior end of the humerus head would pass medial to the level of the scapulo-coracoid, towards the end of the retraction phase, and therefore muscles running between this part of the humerus and the scapulo-coracoid would cease to have a retractive effect. There would be an equivalent, although possibly less marked, tendency for the protractor muscles between the anterior part of the humerus head and the scapulo-coracoid to lose their protractive action towards the end of the protraction phase. The reason for restricting the locomotor muscles to origins from the shoulder girdle itself is probably related to the mobility of the scapulo-coracoid, and the consequent difficulties that would arise if large muscles ran between the humerus and any part of the body in front of, or behind, the shoulder girdle. Muscles that could motivate the system in *Procynosuchus* are discussed below.

The obvious drawback to an arrangement that involves a very small area of contact between the humerus head and the glenoid is that large reaction forces would not be tolerable, for they would tend to damage the joint surfaces. Some alleviation of the problem would be gained by the use of slightly deformable cartilage layers, so that the area of contact became larger, but nevertheless this remains one argument, among several mentioned later, indicating that the forelimb was not primarily used to generate significant locomotory forces.

(*c*) *Elbow joint*

The condyles on the distal end of the humerus are very like those described by Jenkins (1973) in other cynodonts. They extend from the dorsal to the ventral surfaces, and permit a flexion–extension movement of the ulna and radius of over 90°. The ulna certainly can be fitted with its axis almost in line with the humerus axis at one extreme, and at the other making an angle of substantially less than a right angle with the humerus. However, because of the poor state of the radius and ulna, little more can be said of the function of this joint.

(*d*) *Musculature*

Most authors, including Romer (1922) and Jenkins (1971), conclude that the well developed fossa occupying the lateral surface of the typical cynodont scapula indicates the presence of a mammalian-like spinatus muscle, evolved by a dorsal extension of the area of origin of the supracoracoideus muscle of more primitive forms. The reflected anterior edge is regarded as the origin for the deltoideus muscle (and the insertion of the trapezius), homologous to the mammalian scapula spine.

The absence of a fossa in *Procynosuchus*, in contrast, suggests that the spinatus muscle was not present in this particular cynodont. The slight anterior fossa of the lateral scapula surface is not in any way marked off from the anterior edge of the bone, and is therefore interpreted as the area of origin of the deltoideus muscle (figures 7 and 12*b*). A large deltoideus, such as this would imply, corresponds well with the very large delto-pectoral crest of the humerus. On this view, the scapulo-humeralis anterior and supracoracoideus muscle complex, from which the mammalian spinatus muscles evolved, had an origin restricted to the broadly concave, antero-ventral region of the scapula and adjacent procoracoid. The insertion must have been a slight depression and bounding ridge, which lies at the proximal end of the dorsal surface of the humerus, immediately anterior to the bulbous part of the articulating surface. Functionally, the deltoideus would have acted as a rotator of the humerus about its long axis during the recovery phase, as well as an elevator. The proposed scapulo-humeralis anterior and supracoracoideus complex would be primarily a protractor of the humerus. As long as the humerus retained its horizontal, sprawling mode of action, there would be no point in developing a spinatus muscle, for it would only duplicate the action of the deltoideus, and therefore the absence of the spinatus is to be expected in *Procynosuchus*. As it is, the proposed scapulo-humeralis anterior and supracoracoideus complex would act in the manner required of the mechanical arrangement of the shoulder joint. This, as discussed above, is for a protractor attached near to the anterior part of the articulating surface, and directed medially to attach directly to the scapulo-coracoid.

The postero-dorsal fossa of the lateral surface of the scapula blade may indicate the area of origin of a teres major muscle, that is an anterior component of the latissimus dorsi attaching to the scapula rather than to the body fascia posterior to the girdle. Previous authors have also reconstructed such a muscle in cynodonts, although indicating that it was more restricted because of the requirement for a spinatus muscle over most of the scapula. The insertion of the teres major, according to Jenkins (1971), is indicated by a definite groove on the posterior part of the dorsal humerus surface, well distal to the head. No such prominent groove is present in *Procynosuchus*, and it seems reasonable to suggest that the muscle was attached over much of the flat dorsal surface of the proximal end of the humerus. There could not have been a large latissimus dorsi muscle attaching here, because its action would tend to pull the humerus posteriorly out of the glenoid fossa, in the absence of a posterior glenoid buttress of any kind. The action of the teres major would have been as an elevator, and it would also have contributed to rotation of the humerus about its long axis during the power stroke phase of locomotion.

The principal retractor muscles appear to have inserted on the postero-medial corner of the humerus, and constituted the subcoraco-scapularis complex (subscapularis of mammals). One area of origin was probably from the posterior vertical fossa on the internal surface of the scapula, and this component would also have a tendency to rotate the humerus about its long axis, at least during the earlier phases of the power stroke. A second possible area of origin is from the internal surface of the scapula ventral to the fossa, and from the adjacent coracoid. As was seen with the protractor muscles, these retractors insert close to the level of the articulating surface, run largely medially, and attach solely to the scapulo-coracoid. Thus they fulfil the requirements of the proposed mechanism of movement at the shoulder joint (figure 12).

Other muscles of the shoulder region do not require much discussion. The postero-ventral fossa of the lateral face of the scapula is probably the area of origin of the triceps head of the scapula, and the tubercle at the posterior extremity of the coracoid is probably for the coracoid head of the same musculature. The coraco-brachialis and biceps probably originated from the lateral face of the coracoid in much the manner indicated by Jenkins (1971) in other cynodonts,

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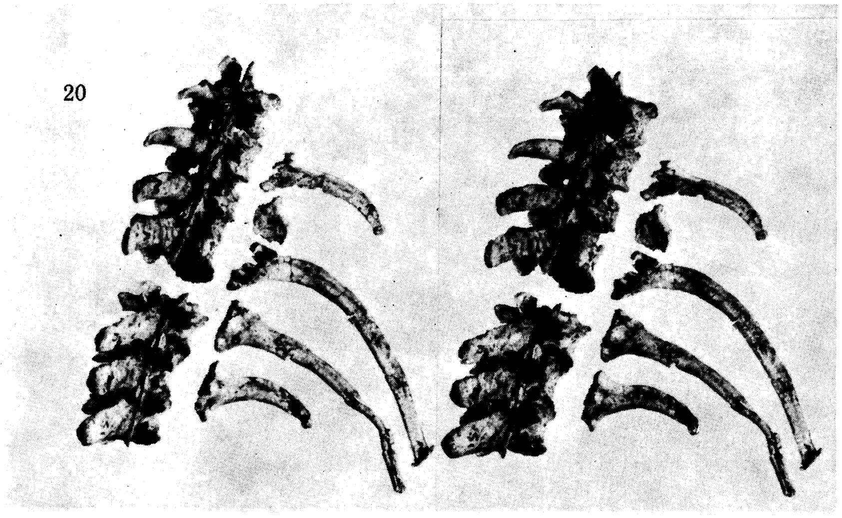

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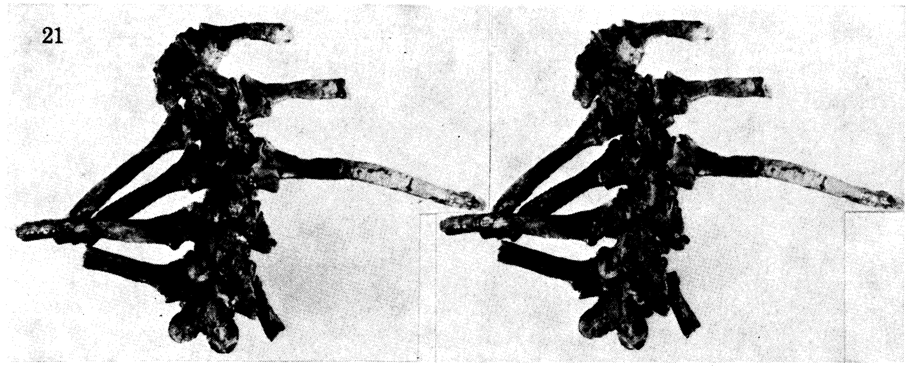

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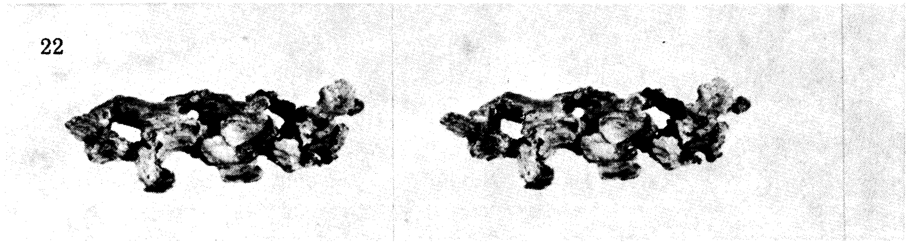

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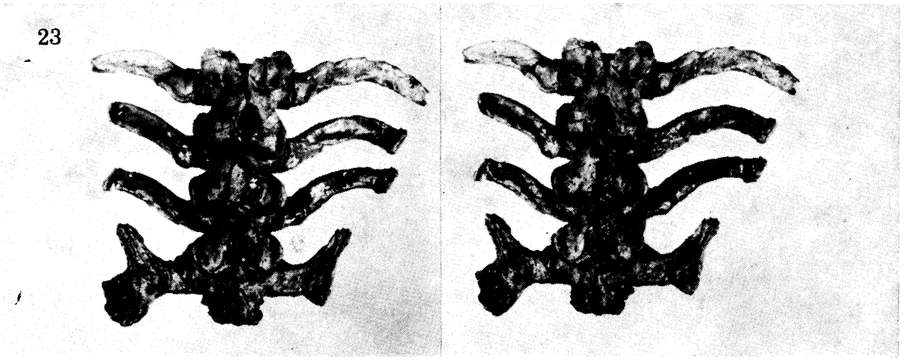

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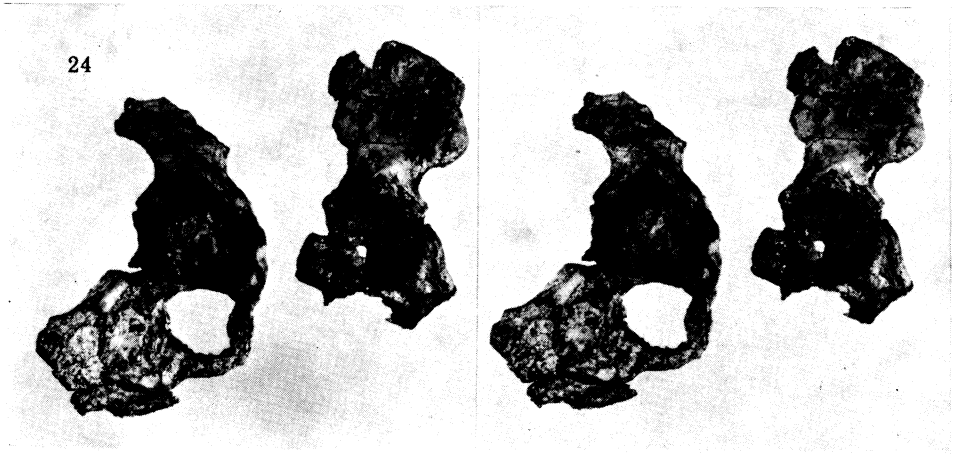
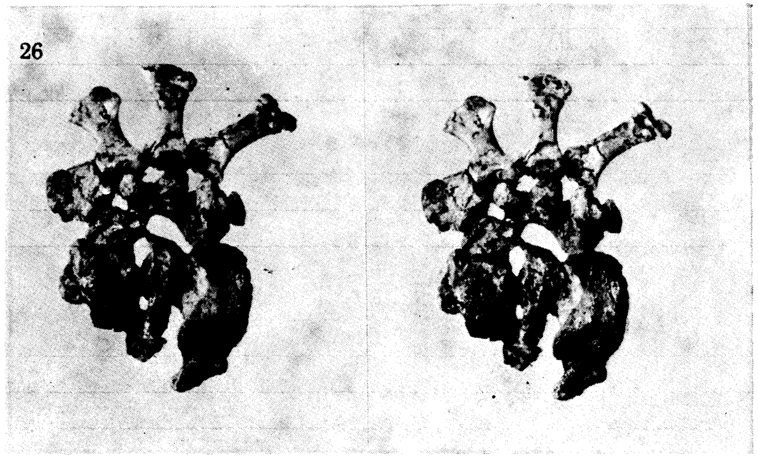
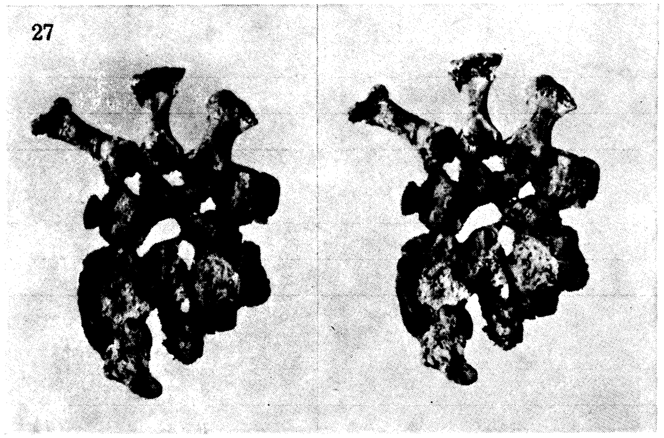


FIGURE 20. Vertebrae 5 to 11, with right ribs 6 to 10. Two-thirds natural size.
FIGURE 21. Vertebrae 16 to 20. Two-thirds natural size.
FIGURE 22. Caudal vertebrae, with haemal arches. Natural size.
FIGURE 23. Vertebrae 26 to 28, and first sacral vertebra. Two-thirds natural size.
FIGURE 24. Right and left pelvic girdles in lateral view. Two-thirds natural size.





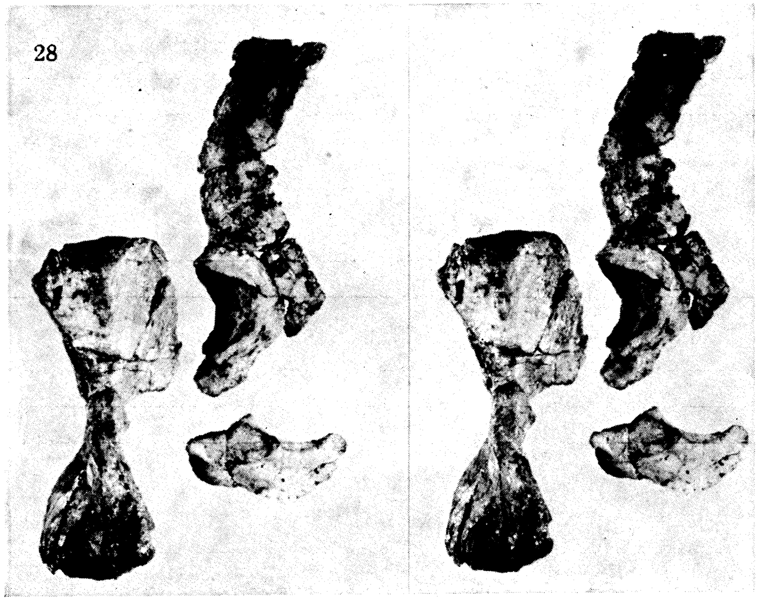


FIGURE 25. Right femur in dorsal view, and left femur in ventral view. Natural size.
FIGURE 26. Right manus in dorsal view. Natural size.
FIGURE 27. Right manus in ventral view. Natural size.
FIGURE 28. Right humerus in dorsal view, right scapulo-coracoid in lateral view, and left coracoid in lateral view. Two-thirds natural size.

since the form of the coracoid is similar in *Procynosuchus*. A large pectoralis was no doubt present, as in all synapsids, inserting on the ventral surface of the delto-pectoral crest. The slight groove on the anterior edge of the scapula blade marks part of the insertion of the trapezius muscle.

(*e*) *The locomotory function of the forelimb and girdle*

The humerus was capable of retraction in a horizontal plane, from almost transverse to fairly close to posteriorly directed. It could rotate about its long axis through almost 90°, and the knee joint was capable of considerable extension. A reasonable degree of elevation and depression of the distal end could occur, particularly including elevation during the recovery stroke. Added to these movements was an undefinable amount of movement of the scapulo-coracoid relative to the rest of the skeleton, including both an anterior–posterior shift, and rotation about a vertical axis through the acromio-clavicular contact. The role of these various components of the locomotory movements can be crudely assessed quantitatively in terms of their contributions to forward movement. Humerus retraction will contribute about one humerus-length to the stride, allowing for the effective increase in humeral length resulting from the form of the glenoid. Rotation of the humerus about its long axis will contribute up to about two-thirds of the radius length, and extension of the elbow joint about the same. Assuming that the radius was about the same length as the tibia, the total forward movement of the body during a single power stroke will be somewhat over two humerus-lengths, or about 33 % of the presacral length of the animal. To this may be added anything up to 10 % of the presacral length for scapulo-coracoid movements. It becomes clear, therefore, that the forelimb of *Procynosuchus* was capable of a perfectly adequate amplitude of stride. Lateral shift of the body towards the foot of the active side will also occur as a result of humerus retraction in the horizontal plane, but this will be at least partly offset by the extension of the elbow joint (assuming that the humerus does not reach a completely posteriorly directed position).

However, despite the suitable amplitude of the stride, several features indicate that the power stroke was not in fact very powerful in terms of providing active locomotory forces. The best developed muscles of the shoulder region of *Procynosuchus*, as of therapsids and primitive reptiles generally, are the deltoideus, which is a recovery stroke muscle, and the pectoralis, which is a postural muscle, although providing some propulsive force by its long-axis rotation function. Muscles primarily concerned with producing the power stroke are the relatively small subcoraco-scapularis and perhaps to a small extent the teres major. As mentioned, there could not have been a significant latissimus dorsi component with a posteriorly directed pull on the humerus, because of the absence of a posterior buttress to the glenoid fossa. Thus no large retractive force acting on the humerus appears to have been possible. The point, or near point, contact between the head of the humerus and the glenoid, although increasing the effective length of the humerus, would not permit the generation of large forces at the shoulder girdle. Also, the fact that the flexor muscles of the lower leg are apparently as well developed as the extensors, to judge from the equal prominence of the ectepicondyle and entepicondyle, suggest that the power stroke of the limb was no more powerful than the recovery stroke. Finally, the humerus is broadly expanded both proximally and distally. Its moment of inertia must have been very much greater than that of the femur, which would tend to reduce the effectiveness of the application of muscle forces to locomotory action. It may be concluded, therefore, that the primary function of the forelimb was as a support for the front part of the body during locomotion, and that its direct contribution to the locomotory force was small. It behaved analogously to the wheel at the front of a wheelbarrow. The extent, if any, to which the forelimb of modern sprawling-gaited animals contributes to the locomotory force is not known. In cursorial mammals, the forelimb does produce a locomotory thrust during the later stage of the stride, of comparable magnitude to that of the hindlimb (Manter 1938; Jayes & Alexander 1978). The view of forelimb function in *Procynosuchus* presented here explains many of the otherwise odd features of the forelimb as discussed. It also accounts for the well known paradox that while the hindlimb of cynodonts evolved quite radically from the primitive, pelycosaurian condition, the forelimb shows relatively little change. The only modifications of the forelimb are to increase the amplitude of the stride, while the hindlimb has improved in terms of the forces of locomotion it generates as well.

Thus far, *Procynosuchus* has been interpreted as a terrestrial tetrapod. However, certain features of the axial skeleton and hindlimb show that it was also capable of effective aquatic locomotion. Therefore, some of the differences between the forelimb and girdle of *Procynosuchus* and other cynodonts may be accounted for by this. In particular, the manifestly greater freedom of movement of the humerus in the shoulder girdle that results from the postero-ventrally facing rather than horizontal scapular glenoid, may be attributable to an aquatic function. The very flat nature of the radius, ulna, manus and possibly of the humerus itself may also be related to their use in water.

On the other hand, some features of *Procynosuchus* forelimb are probably primitive with respect to later cynodonts. The most striking example is the absence of a spinatus muscle coupled with retention of a large scapula component of the deltoideus, which resembles the condition in other therapsids and their pelycosaur ancestors.

D. THE PELVIC GIRDLE AND HINDLIMB

1. *Description*

(*a*) *The pelvic girdle*

The two sides of the pelvis are preserved (figure 13; figure 24, plate 1) and were joined along part of the ischiadic symphysis. However, most of the right ilium, the left ischium and both pubes are missing. The reconstructions are composites of the two sides.

As preserved, the left ilium is very short and lacks distinct anterior and posterior extensions. Parts of the edges may, however, be incomplete, despite the apparently smoothly rounded finish they have. Thus, a more typically cynodont shape of the ilium cannot be excluded, and certainly a longer ilium is necessary if the four or even five sacral vertebrae believed to have been present were to have attached to the pelvis. Nevertheless, the notches in the margin of the ilium between the dorsal blade and the acetabular region, both anterior and posterior, are much less acute than in later cynodonts. This suggests that a significantly shorter ilium was in fact present. Practically the whole of the lateral surface of the ilium blade is a single, shallow fossa, as in the later forms. The medial face of the ilium blade is also very slightly concave, and has a series of fine striations in the antero-dorsal region. There are no scars or other indications of the sites of contact of the sacral ribs with the pelvis. A feature that has not been described in other cynodonts is a slight recessing of the antero-ventral part of the internal iliac surface, which is continuous with the internal surface of the pubis below. It is interpreted as the area of origin of the pubo-ischio-femoralis internus musculature.

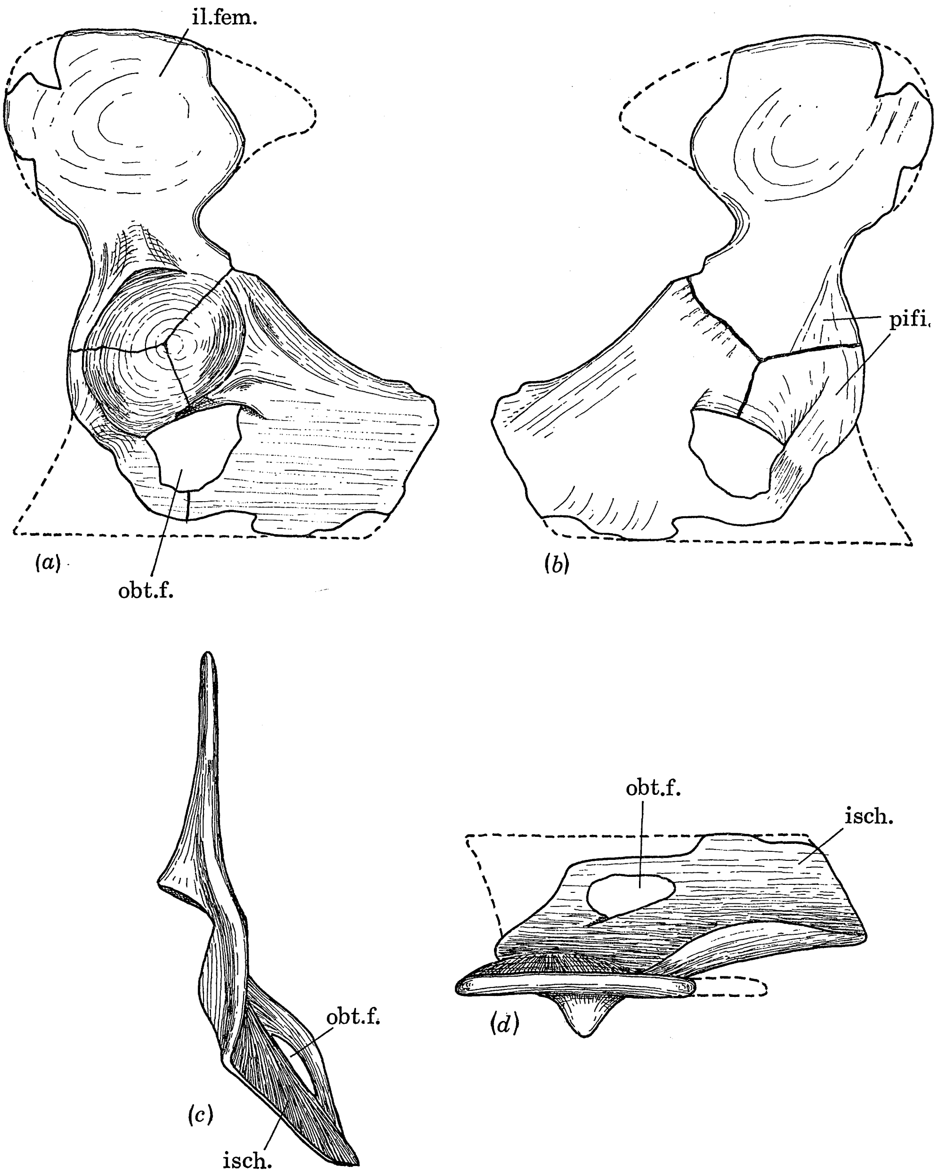


Figure 13. Pelvic girdle (composite, drawn as left). (*a*) Lateral view; (*b*) medial view; (*c*) posterior view; (*d*) dorsal view. Natural size. Abbreviations: il. fem., origin of ilio-femoralis muscle; isch., ischium; obt.f., obturator fenestra; pifi., origin of pubo-ischio-femoralis internus muscle.

The ischium is a relatively very large, flat plate, strengthened by a prominent external ridge below and parallel to the dorsal margin. A large obturator fenestra is present. Its margins are extremely thin and clearly graded into a membrane across the hole. The medial face of the ischium is also very smooth and featureless. It is slightly concave from top to bottom, and also flares laterally to a small degree in its posterior region. Ventrally, the ischia meet along a symphysis that is horizontal and very thin.

The left pubis is represented only by its acetabular component, and the right by the same, plus a strip bounding the obturator fenestra. Ventral to the powerful dorsal ridge that buttresses the acetabulum, the pubis lies at a more medial level, in the same plane as the ischium. The medial surface of the pubis is flush with the recessed antero-ventral region of the ilium.

The acetabulum is very much broader and shallower than in other cynodonts. All of the three component bones contribute stout buttresses, extending laterally to the main plane of the pelvis. Of these, the iliac buttress is the best developed, and its articulating surface forms an angle of about 55° to the plane of the pelvis. The pubic and ischiadic buttresses are less developed, and their articulating surfaces are only at about 20° to the pelvic plane. Between these respective buttresses, the edge of the acetabulum is barely raised at all. The overall effect is of a shallow, perfectly spherical socket facing almost exactly laterally. All of the parts are smoothly confluent with one another. In other cynodonts, by contrast, the acetabulum is deeper, of relatively smaller diameter, and the articulating faces of the three contributing bones tend to be more distinctly separated from one another by changes in angles.

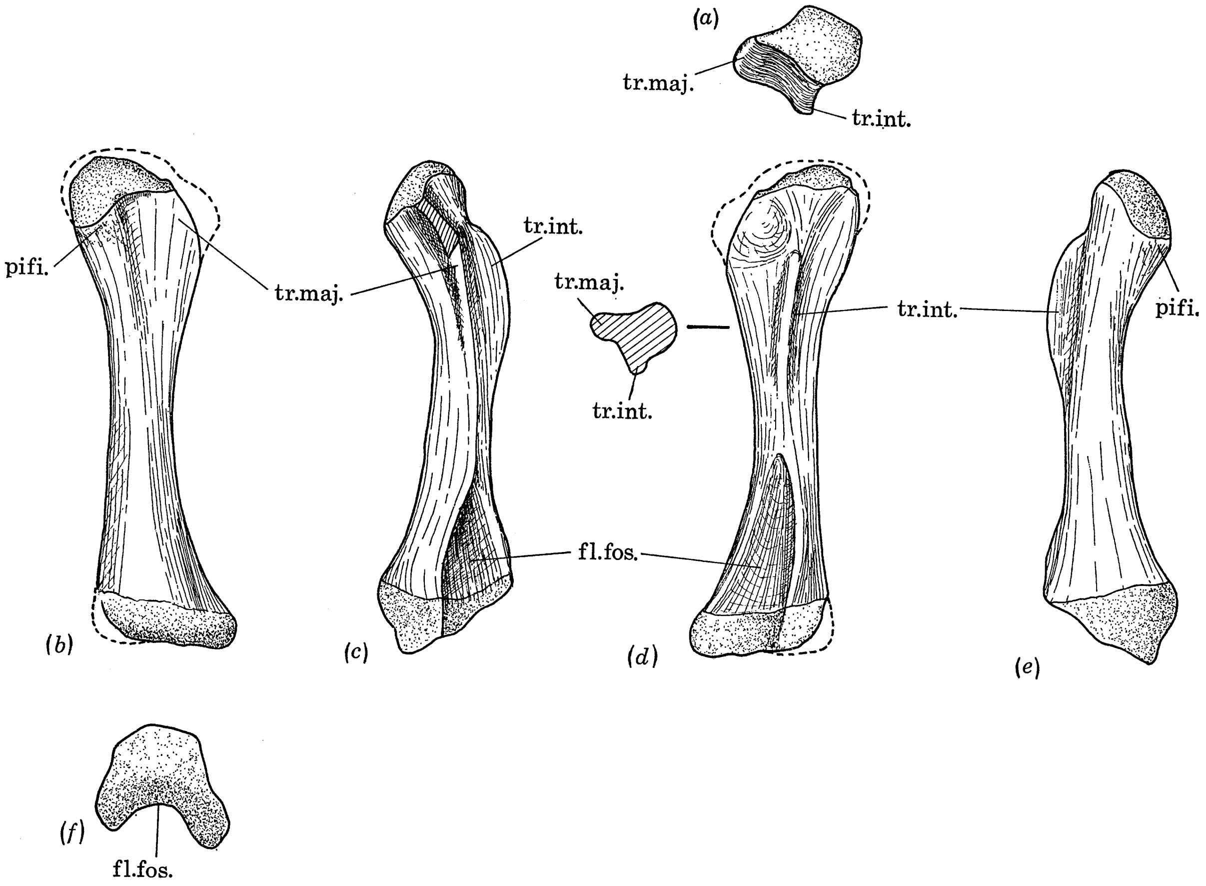


FIGURE 14. Femur (composite, drawn as left). (*a*) Proximal view; (*b*) dorsal view; (*c*) lateral view; (*d*) ventral view with transverse section as indicated; (*e*) medial view; (*f*) distal view. Natural size. Abbreviations: fl. fos., flexor fossa; pifi., insertion of the pubo-ischio-femoralis internus muscle; tr. int., trochanter internus; tr. maj., trochanter major.

(*b*) *The femur*

The right femur is well preserved, but has lost the proximal end of the head and trochanter major. The complete proximal end, and the distal half of the left femur, are present, but have suffered from weathering and some distortion. The reconstruction is a composite made by using both femora (figure 14; figure 25, plate 2).

The femur of *Procynosuchus* has the same basic structure of other cynodonts, but at the same time possesses a number of unique characters of its own. The head is apparently less inturned medially, and the trochanter major less laterally reflected than in the well ossified femora described by Jenkins (1971). However, because of the rather poor preservation of the left head, there is some doubt about this interpretation. What is more sure is that the trochanter major is a thinner, longer flange that is more clearly separate longitudinally from the main shaft of the femur. In dorsal view particularly, there is a deep grooving between the trochanter major and the shaft, whereas in other cynodonts the dorsal surfaces of the trochanter and of the shaft are continuous with one another.

The internal trochanter of the present femur is slightly more posteriorly placed on the ventral surface than in other cynodonts.

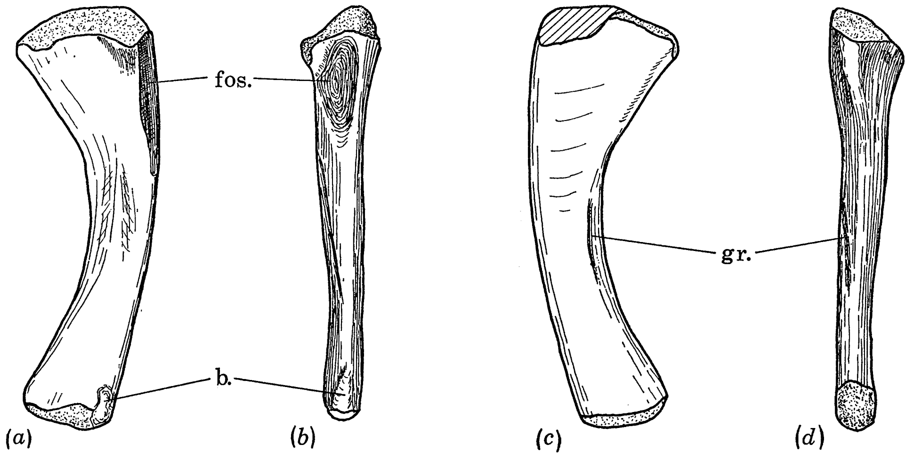


FIGURE 15. Tibia (right). (*a*) Anterior view; (*b*) medial view; (*c*) posterior view; (*d*) lateral view. Natural size. Abbreviations: b., boss; fos., medial fossa; gr., groove.

Comparing the proximal and distal ends of the bone, the shaft of the femur twists so that if the proximal end is aligned horizontally, then the distal condyles face postero-ventrally at about 45° to horizontal. The distal condyles themselves, crushed in the left femur but well preserved if a little incomplete in the right, are much deeper dorso-ventrally than in other cynodonts. A very deep fossa for the flexor muscles of the lower leg occupies the ventral surface. This is one of the most marked differences between the femur of *Procynosuchus* and of the later cynodonts.

(*c*) *The tibia*

The complete right tibia (figure 15) and a large part of the left tibia are preserved. The bone is considerably more curved than in other cynodonts, and is also rather flatter. Assuming an orientation of the bone in the fully protracted limb position, the anterior face consists of a flat, expanded proximal end, with a prominent process on the medial corner. A ridge runs from the medial edge down the bone, to peter out along the lateral margin about two-thirds the way down the bone. The bone medial to the ridge is a shallow, vertical fossa. The distal end of the anterior face is flat, and bears an irregular boss on its medial corner.

The narrow medial face of the tibia is dominated by a very deep fossa, occupying the proximal end. The posterior margin of the fossa is sharp, and the anterior margin more rounded. The fossa attenuates about 2 cm down the shaft. The posterior face of the bone is flat, and the lateral margin of the proximal end is slightly raised. In the middle of the shaft is a prominent groove. The distal end of the bone in this view is convex from side to side. The lateral face is in fact little more than a fairly sharp edge.

The proximal articulating surface is poorly ossified, or poorly preserved, and probably does not reflect accurately the form of the articulation surface in life, other than the pyriform outline shape. The distal facet for articulation on the astragalus is a very flattened oval, with the prominent tubercle on its anterior–medial corner, mentioned above.

(*d*) *The fibula*

The fibula (figure 16) poses a problem because, although one almost complete fibula and the two ends of the other are present and well preserved, this bone differs so markedly from that of other cynodonts that orientation of the bone by comparison is impossible. Jenkins (1971) comments upon the great variability of this bone among other cynodonts.

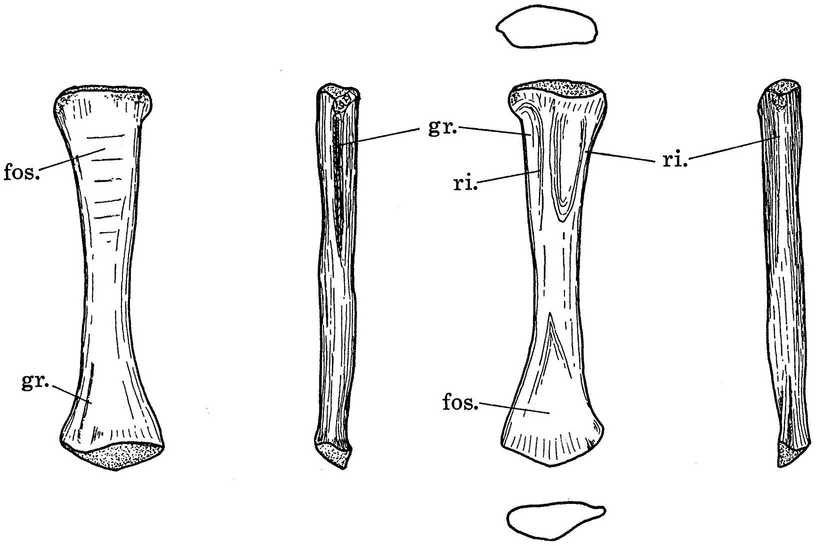


FIGURE 16. Fibula (composite, orientation unknown). In four views, with outlines of the ends indicated. Natural size. Abbreviations: fos., fossa; gr. groove; ri., ridge.

The most immediate feature of *Procynosuchus* fibula that contrasts with the other forms is its straightness and flatness.

2. *Functional interpretation*

(*a*) *Orientation and movements of the femur*

Unfortunately, the only head of a femur present, the left, is not sufficiently well preserved to allow an exact assessment of possible movements of the femur in the acetabulum. What is certain, however, is that the radius of curvature of the broad, shallow acetabulum far exceeds that of any possible femur head, unless an absurdly large layer of cartilage covering the acetabulum is postulated. Thus, the femur appears to have had a wide range of possible movements. If the femur is placed horizontally in the acetabulum, as in a primitive, sprawling-gaited animal (figure 17*a*, *b*), protraction to a position almost parallel with the axis of the body is possible. Retraction is limited by the tendency for the trochanter major to contact the posterior edge of the acetabulum. However, this trochanter lies adjacent to the posterior notch between

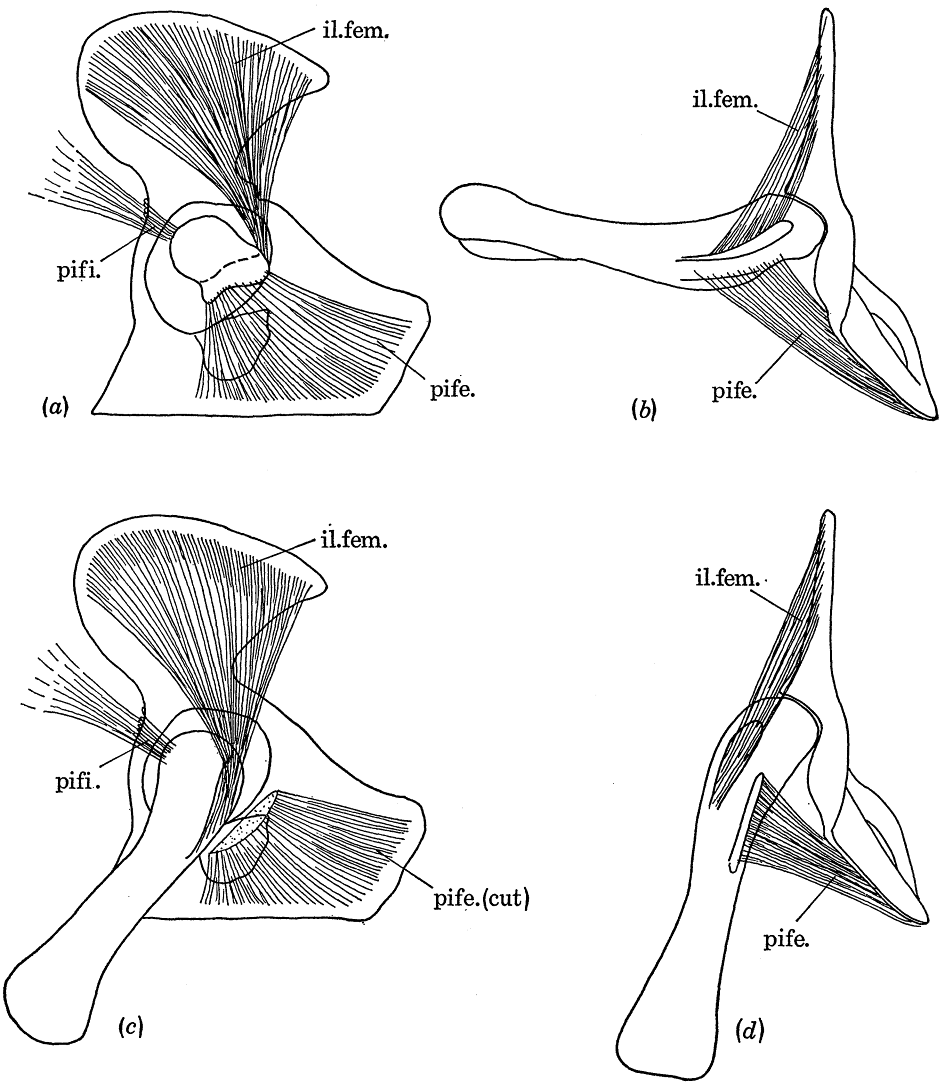


FIGURE 17. Function of the hip joint. (*a*) Orientation of the femur and major muscles during the sprawling gait, in lateral view; (*b*) the same in posterior view; (*c*) orientation of the femur and major muscles during the erect gait, in lateral view; (*d*) the same in posterior view. Abbreviations: il. fem., ilio-femoralis muscle; pife., pubo-ischio-femoralis externus muscle; pifi., pubo-ischio-femoralis internus muscle.

the iliac and ischiadic buttresses, and therefore the femur can still retract beyond the transverse position. During this arc of movement of the femur, there is no mechanical limit to rotation of the bone about its long axis, and considerable elevation and depression (adduction) is also possible.

The femur can also be moved in an arc corresponding to a semi-erect, or almost erect, gait (figure 17*c*, *d*). With the distal condyles of the femur orientated transversely, the femur can start its movement from a horizontal orientation at an angle of around 30–35° to the body axis. From here, the distal condyles can swing postero-ventrally in a very mammal-like fashion to a position behind the transverse plane.

(*b*) *Hip musculature*

The single, shallow fossa occupying the whole of the lateral surface of the ilium indicates the origin of the ilio-femoralis (mammalian gluteal) muscle (figure 17), and its insertion was undoubtedly the dorsal and lateral parts of the trochanter major. Neither of these sites of muscle attachment were as well developed as in later cynodonts, indicating that the ilio-femoralis muscle was smaller.

There is no evidence for part of the origin of the pubo-ischio-femoralis internus (mammalian psoas–iliacus complex) having reached the lateral surface of the ilium. This is in contrast to Parrington's (1961) suggestion, and to the condition in therocephalian therapsids (Kemp 1978). There is, however, a distinct fossa occupying the internal surface of the pubis and extending on to the internal surface of the antero-ventral part of the ilium (figure 13). This must be for the pubo-ischio-femoralis internus, and indicates that it had begun a dorsal migration. What remains unknown is whether this muscle also had fibres originating anterior to the pelvis, from the fascia of the flank, or the lumbar ribs. This occurs in mammals, and also in crocodiles, and is therefore perfectly possible. The reduction and rigid attachment of the lumbar ribs may be related in part to such a development. The insertion of the pubo-ischio-femoralis internus in cynodonts has led to some argument, as reviewed by Jenkins (1971). Parrington (1961) believed that the muscle inserted on the internal trochanter, and that this trochanter was therefore the equivalent of the mammalian trochanter minor. Romer (1922), followed by Jenkins (1971), claimed that the muscle attached to the dorsal and medial parts of the proximal end of the femur, but its insertion did not extend ventrally as far as the crest of the internal trochanter. In *Procynosuchus*, a pubo-ischio-femoralis internus muscle, originating from the area suggested, could not possibly have inserted on to the crest of the internal trochanter. With the femur in a sprawling position, this trochanter lies mid-ventrally. With the femur in a more erect position, the trochanter lies almost posteriorly. It appears, therefore, that the muscle must have inserted as Jenkins suggests, on the dorsal and medial parts of the femur head. The surface of the bone is rugose here (figure 25, plate 2), although in part this might have been the result of the weathering. At most, the insertion may have occupied the medial face of the internal trochanter.

The very large ischium indicates that the pubo-ischio-femoralis externus (mammalian obturator externus) was a large muscle, and particularly well developed posteriorly. Its insertion must have been centred on the crest of the internal trochanter, although presumably it extended laterally on to the ventral surface of the trochanter major.

The size of the caudi femoralis muscle complex is of the greatest interest, in view of its eventual decline in the line leading to the mammals, but it is impossible to assess reliably. The size of the caudal vertebrae, and the length of the tail, indicate that there is available an adequate area of origin for a caudi femoralis. However, there is no clear insertion site on the femur. No well developed equivalent of the reptilian fourth trochanter is present. It could be represented by the more distal part of the internal trochanter, but this is so fine that the muscle must be assumed to have been small.

(*c*) *Locomotory function of the hindlimb*

Gregory (1912), Gregory & Camp (1918) and Romer (1922) established the idea that a profound modification of the hip musculature occurred between a reptilian and the mammalian conditions, and that this was functionally correlated with the change in stance and gait. The ilio-femoralis muscle enlarged, particularly anteriorly, to replace the reptilian caudi femoralis as the main retractor muscle of the hind limb. It is the homologue of the mammalian gluteal muscle complex. At the same time, the reptilian pubo-ischio-femoralis internus muscle shifted its origin dorsally, from the inner surface of the pubo-ischiadic plate to the ilium, and fascia and ribs of the lumbar region. It is the homologue of the mammalian psoas–iliacus muscle complex. Muscles from the pubis were reduced, along with that bone, but the ischium muscles were retained. The pubo-ischio-femoralis externus is the homologue of the mammalian obturator externus, from the outer face of the ischium. The ischio-trochantericus is the homologue of the mammalian obturator internus, from the inner face of the ischium. These alterations were related to the shift from the sprawling gait of the reptilian level to the erect gait of typical mammals, and indeed can be shown to be necessary changes for the development of the new gait at all.

Cynodonts show an intermediate anatomy in many ways, with the enlarged ilium and trochanter major for the ilio-femoralis muscle, a reduced pubis, but still a large ischium. The question of whether the internal trochanter of the femur is the homologue of the mammalian trochanter minor, evolved for insertion of an enlarged pubo-ischio-femoralis internus muscle, has been debated. Parrington (1961) regards this as the case, and suggested that this muscle had achieved a more dorsal origin, from the ilium blade. Jenkins (1971), following Romer (1922) denies this point, while nevertheless accepting the intermediate nature of the cynodont hindlimb anatomy.

All of these authors argue that the intermediate anatomy indicates that the stance and gait of cynodonts was geometrically intermediate between sprawling and erect. Jenkins (1971) was the first to consider the exact nature of the locomotory function of the cynodont hindlimb, making use of comprehensive, well preserved postcranial material. He claimed quite specifically that the cynodont femur moved in an arc about 50° to the body axis. I have recently suggested an alternative view of the intermediate stages between a primitive sprawling gait and a mammal-like erect gait (Kemp 1978). With reference to a specimen of a therocephalian therapsid, it appears that two distinct gaits were possible, rather as in modern crocodiles. On the one hand, the animal could adopt a typically sprawling gait, but equally could choose to use a near-erect gait. The evidence for this view involved the nature of the hip joint, the shape of the femur and the structure of the ankle joint. It can also be demonstrated that the hip musculature, reconstructed on the basis of the anatomy of the bones, was suitably arranged to permit locomotion by either gait. Overall, this dual-gaited condition is a more satisfactory intermediate condition than a single, specific intermediate gait. It reflects the fact that evolution of locomotion in the mammal-like reptiles was concerned primarily with increasing the adaptability of the locomotory apparatus, and not with increasing efficiency or speed *per se*. In modern forms at least, it seems to be impossible to demonstrate that the sprawling gait is either less efficient or slower than the basic mammal gait by virtue of the different geometrical arrangement of the bones and muscles involved.

In *Procynosuchus*, evidence from the ankle is unfortunately wanting, but the nature of the rest of the pelvic and hindlimb bones indicates that it too probably had a dual-gaited locomotory pattern.

The mechanical possibility of the femur moving in a horizontal, sprawling-gaited manner in the acetabulum has been noted. The musculature can also be shown to have been appropriate for this kind of locomotion (figure 17*a*, *b*). Retraction would have been by the evidently well developed pubo-sichio-femoralis externus, and, to the extent that it may have been present the caudi femoralis. Rotation of the femur about its long axis during the power stroke would be performed mainly by the ilio-femoralis muscle pulling more or less dorsally on the trochanter major. Long axis rotation was probably a significant component of the power of the locomotory cycle. In any sprawling-gaited animal, long axis rotation must occur if the crus is to slope forwards at the beginning of the active stride, and backwards at the end of it. However, in *Procynosuchus*, as in other therapsids, the overall locomotory force has been increased by arranging the muscles to provide a more powerful, active rotation. As discussed later, this may be in part compensation for a reduction in the component of locomotion associated with lateral undulations of the body.

The recovery stroke of the sprawling gait was largely made by the pubo-ischio-femoralis internus muscle, in the standard manner of sprawling tetrapods. Thus, the ability of *Procynosuchus* to move in this manner is correlated with the retention of the primitive features still to be found in the structure of the pelvis and hindlimb.

In contrast, the possibility of an erect type of gait is related to the evolutionary innovations of the pelvis and hindlimb, and particularly the development of an enlarged ilio-femoralis muscle. That the femur was mechanically capable of rotating in the acetabulum in a plane approaching a parasagittal plane has been indicated. When the distal condyles are arranged in a transverse line, and the femur extends antero-ventrally and slightly laterally from the acetabulum, the trochanter major lies postero-lateral to the head of the femur (figure 17*c*, *d*). The line of action of the ilio-femoralis muscle fibres passes posterior to the centre of rotation of the femur head in the acetabulum, but not significantly lateral to this point. Therefore the action of this muscle is almost entirely to retract the femur in a mammalian fashion. The internal trochanter lies postero-medially, and therefore fibres of the pubo-ischio-femoralis externus muscle will also have a retractive effect, along with an adductive action. However, both these muscles will lose almost completely any tendency to rotate the femur about its long axis.

The recovery phase during erect locomotion would, as in the sprawling mode, involve the pubo-ischio-femoralis internus muscle. However, the most effective fibres will be the more dorsal ones, for they attach more nearly at a right angle to the axis of the femur during the later phases of protraction. Thus the tendency noted in *Procynosuchus* to expand this muscle dorsally onto the antero-medial region of the ilium, reflects the adoption of a facultative erect gait. Possible fibres of this muscle originating from the lumbar region of the animal would also be particularly well disposed for this action.

It is concluded therefore, that the hindlimb was capable of operating in either a primitive, sprawling gaited manner, or in a more mammal-like gait. The significance of these two respective modes of locomotion is discussed in the context of the overall adaptation of the postcranial skeleton for locomotion, in the next section.

Also to be considered there is the role of the hindlimb in aquatic locomotion.

E. LOCOMOTION IN *PROCYNOSUCHUS*

1. *Summary of the most significant features of the postcranial skeleton*

The following points bearing on the methods of locomotion have been established in the previous sections.

(i) The presacral axial skeleton was capable of very limited, if any lateral flexion, except for the lumbar region, which was specialized for extreme lateral movements of the vertebrae relative to one another.

(ii) The tail was well developed, with elongated haemal arches.

(iii) The forelimb was only capable of a sprawling gait, with the humerus moving in a horizontal plane. Nevertheless a large stride was possible, and a reasonable degree of elevation–depression and long axis rotation of the humerus was permitted.

(iv) The forelimb was incapable of generating significantly large locomotory forces, and functioned primarily as a means of support of the front part of the body during motion.

(v) The radius, ulna and forefoot were flattened.

(vi) The hindlimb was capable of operating in both a sprawling gaited manner with the femur horizontal, and a more erect gaited manner with the femur approaching the parasagittal plane.

(vii) A high degree of mobility was permitted at the hip joint.

(viii) The tibia and fibula were very flattened and the flexor muscles between the femur and the crus were powerfully developed.

Several of these points appear to have been adaptations for aquatic locomotion, indicating that *Procynosuchus* was an amphibious animal capable of efficient locomotion in water as well as on land.

2. *Terrestrial locomotion*

The primitive, sprawling mode of locomotion was performed obligatorily by the forelimb and facultatively by the hindlimb. The arrangement of the muscles in both cases indicates that active rotation of the propodium about its long axis, causing the epipodium to rotate from antero-ventrally to postero-ventrally orientated, was an important part of the mechanism. In primitive tetrapods, the action of the limbs is supplemented by lateral undulations of the body, which has the effect of increasing the stride, and probably the total power of the locomotory cycle. However, it has certain fairly obvious disadvantages, since the high lateral components of the forces involved lead to inefficient coupling of the work of the axial muscles to useful locomotory effect. Lateral undulation probably also interferes with the manoeuverability of the animal. In the case of *Procynosuchus* and probably other therepsids and cynodonts, lateral undulation of the vertebral column has been reduced and probably played no significant role in locomotion. The adoption of more powerful long axis rotation of the propodials, particularly of the femur by enlargement of the ilio-femoralis muscle, may be a compensation. In the particular case of *Procynosuchus*, extensive lateral undulations of the lumbar region were possible, but this is interpreted as an adaptation for aquatic locomotion. Because the rest of the dorsal vertebral column was not capable of significant lateral undulation, it is concluded that even in this form, such action of the lumbar region was not used in terrestrial locomotion.

By analogy with modern crocodiles, the sprawling gait was probably used for slow, leisurely movements, keeping the profile of the body low and inconspicuous. It would have been par-

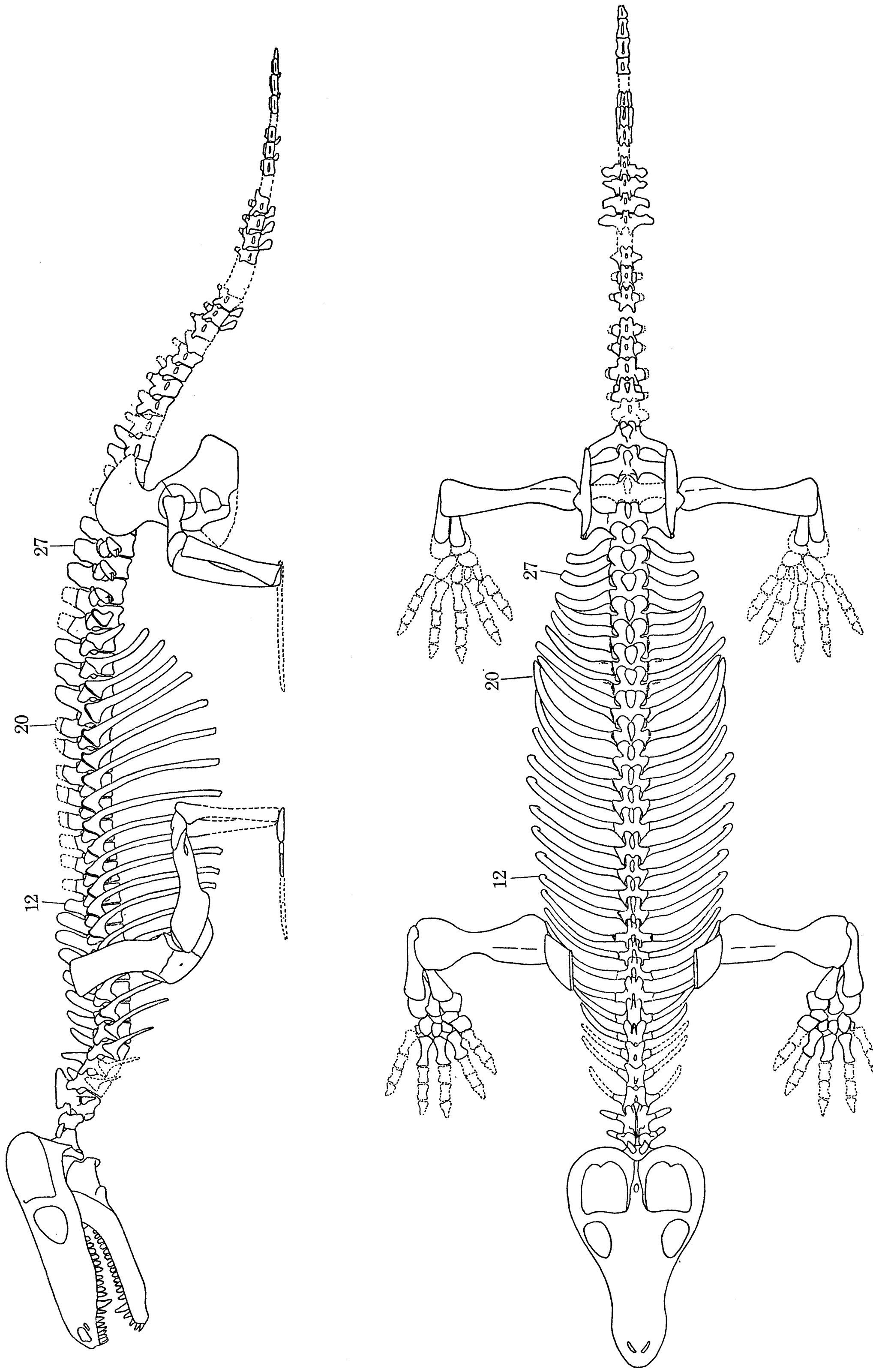


FIGURE 18. Reconstruction of the skeleton of *Procynosuchus delaharpeae*. About two-fifths natural size.

ticularly suitable for traversing soft, muddy stretches adjacent to the banks of rivers and lakes, for the belly would be more or less on the ground.

The erect gait was exclusively a facultative ability of the hind limb. The humerus could not possibly have moved in a near vertical plane without disarticulation of the shoulder joint, or else by having the scapula blade slope postero-dorsally. However, this discrepancy between the forelimb and the hindlimb is not unexpected if, as argued earlier, the forelimb produced very little active locomotory forces. If its function was largely restricted to support of the front part of the body off the ground, then the only requirement of the forelimb is that it could produce a stride length and stride frequency equal to that of the hindlimb. Adaptations for increasing the length of the stride of the forelimb have been discussed earlier, and include both a mobile scapulo-coracoid, and the peculiar geometry of the articulating surfaces of the shoulder joint. In contrast, the hindlimb would be expected to evolve adaptations to increase the locomotory forces it produced, as well as increased stride.

The exact significance of the erect gait of the hindlimb is not clear, even among living animals (Kemp 1978). Neither the efficiency nor the top speed of locomotion differs significantly between similar sized living lizards and living primitive-limbed mammals (Bakker 1975). In fact the clearest distinction between locomotor ability of these two types is the higher rate of aerobic respiration, and hence of sustained running, in the mammals. This is a function of the physiological differences and does not relate to the geometrical arrangement of the limbs. Nevertheless, it remains possible that the distinction between the two gaits of an individual *Procynosuchus* lies in a greater efficiency or speed of the erect gait. A possible factor is the structure of the ankle joint, for in the sprawling gait, more complex stresses are applied to the ankle than in the erect gait (Kemp 1978). Thus it might have been possible to generate greater locomotory forces without damage to the ankle joint when using the erect gait. Manoeuvrability may also have been enhanced with the erect gait, for the hind feet lie closer to the midline of the body. Certainly by comparison with modern crocodiles, it would be expected that the erect gait functioned for faster running, and for longer distance journeys.

3. *Aquatic locomotion*

Certain features of the postcranial skeleton of *Procynosuchus* are both unique, not being found in any other known therapsids, and also difficult to account for as adaptations for terrestrial locomotion. The particular characters are the wide, horizontal zygapophyses of the lumbar region, the elongated haemal arches of the tail vertebrae, the flattened form of the lower limb bones and manus (the pes is unknown), and the prominence of the flexor fossa of the distal end of the femur. Taken together, these specializations suggest that the animal was adapted for swimming, in addition to terrestrial locomotion.

The lumbar region of the vertebral column was clearly capable of very extensive lateral bending. In the absence of an equivalent bending of the thoracic region of the vertebral column, it is difficult to see how the lumbar movements could have aided terrestrial locomotion. In water, however, the lateral movements of the lumbar region would have imparted a lateral undulation to the tail, producing an anguilliform propulsive thrust. Large modern aquatic reptiles, such as crocodiles and monitors, possess rather similar zygapophyses to those of the lumbar region of *Procynosuchus*, and in them a proportion of the lateral undulation of the tail arises in that region of the vertebral column. An analogous mechanism of caudal swimming has been described in the river otter *Lutra canadensis* (Tarasoff *et al.* 1972), although in this case the lumbar vertebrae bend in the sagittal plane, imparting a dorso-ventral undulation to the tail. The sacrum is capable of swinging through an arc of 90° as a result of the mobility of the sacral vertebrae, and clearly the sacrum of *Procynosuchus* could have achieved an equal excursion, albeit in a horizontal plane. The tail itself of *Procynosuchus* is much longer than in any other cynodont, or Upper Permian therapsid, and the curiously elongated, firmly attached haemal arches would have increased the strength and lateral surface area. Again, there is no obvious relation between a long, strong tail and terrestrial locomotion of the therapsid pattern.

Swimming by means of the limbs may also have occurred, and again a comparison with *Lutra canadensis* is instructive. Here, either all four limbs or just the hindlimbs may be used. The action of a single limb consists of a retraction with the limb held in the typically mammalian erect orientation. The foot is aligned vertically and the webbed digits are spread. The recovery stroke consists of protraction of the limb, with the lower segment flexed. The foot therefore trails passively forwards, with the digits closed. The flattened lower limb bones and manus of *Procynosuchus* suggest that a similar limb swimming occurred. Many aquatic tetrapods tend to flatten their limb bones, to use them as paddles. The peculiar superposition of the proximal centrale and third carpal on the ulnare and fourth carpal respectively might represent a stiffening of the manus against the pressure of the water. Powerful backthrust of the femur in water would tend to cause the tibia and fibula to bend forwards relative to the femur, dislocating the knee joint. Strong flexor muscles behind the knee would be required to prevent this, and therefore the flexor fossa of the femur is much better developed than in purely terrestrial relatives of *Procynosuchus*.

Thus, although no single modern animal shows the same suite of apparently aquatic adaptations as *Procynosuchus*, nevertheless an *a priori* argument from structure to function indicates the likelihood that it was a proficient, relatively highly adapted swimmer. The possibility exists that the erect gait of *Procynosuchus* was not used for terrestrial locomotion at all, but existed purely as an adaptation for swimming. However, since those features that lead to the conclusion that *Procynosuchus* was capable of an erect type of gait are those evolutionary modifications present in the undoubtedly non-aquatic later cynodonts, there is no reason to believe that *Procynosuchus* was not capable of a similar kind of advanced terrestrial locomotion as these later forms.

The existence of suitable aquatic conditions within the area where this specimen of *Procynosuchus* lived is indicated by the presence of freshwater fish at a nearby locality (Kemp 1975). These include both hybodont sharks and *Acrolepis*-like palaeoniscids.

F. THE EVOLUTIONARY SIGNIFICANCE OF THE POSTCRANIAL SKELETON

1. *Phylogenetic relationships of Procynosuchus*

The phylogeny of the main genera of pre-Middle Triassic cynodonts, including *Procynosuchus*, was discussed in the previous paper on this specimen (Kemp 1979), with conclusions indicated in figure 19. The evidence used was mainly cranial, but the major postcranial features were also considered. It is now clear that the *Procynosuchus* postcranial skeleton consists of a mosaic of characters primitive for the cynodonts (plesiomorphs), characters shared with the later cynodonts (synapomorphs), and characters unique to *Procynosuchus* (autapomorphs).

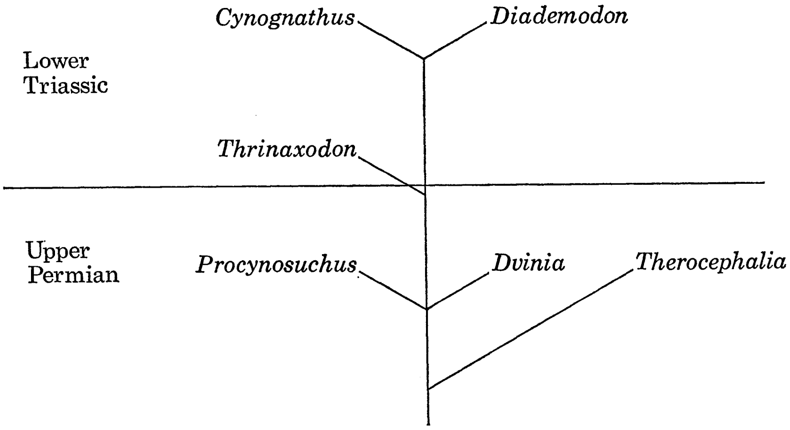


FIGURE 19. Phylogeny of pre-Middle Triassic cynodonts.

2. *Plesiomorphic characters*

Based on a comparison between the later cynodonts on the one hand, and the other therapsids, particularly therocephalians, on the other, the following characters of *Procynosuchus* are judged to be plesiomorphic.

Absence of accessory zygapophyseal articulations on the vertebrae.
Parapophyseal articulations of ribs not shared by adjacent centra.
Ribs lacking expanded costal plates.
Ribs of the anterior lumbar region with long shafts, extending the rib-cage posteriorly.
(Possibly only four sacral vertebrae)
Well developed tail.
No spinatus fossa on scapula blade.
Glenoid less restrictive.
Coracoid plate larger.
Ilium less expanded anteriorly.
Ischium larger (size of pubis is unknown).
Trochanter major smaller, and less set off from femoral shaft.

It is considered improbable that any of these characters have reverted to a primitive-like condition from the fully expressed cynodont condition. Besides the direct comparisons, the early appearance of *Procynosuchus* adds some further support to the present interpretation. Also, the relatively large number and diverse nature of these characters would imply an astonishing degree of evolutionary reversion.

Functionally, the primitive characters retained by *Procynosuchus* reflect the continued presence of the sprawling gait pattern of locomotion.

3. *Cynodont synapomorphic characters*

The following characters of *Procynosuchus* are found in the later cynodonts, but not generally in other therapsid groups.

Structure of the atlas–axis complex.
Reduction of the neural spines of the cervical vertebrae.
Differentiation into thoracic and lumbar vertebrae.

Formation of synapophyses by confluence of the diapophyses and parapophyses.
Trough-and-peg type zygapophyses in the dorsal region.
Short, near-horizontal lumbar ribs, immovably attached to vertebrae.
Some degree of anterior expansion of the ilium.
Arrangement of the trochanters of the femur.

There is no evidence that any of these characters evolved in parallel with the changes in the main cynodont line. Functionally, they reflect among other things the adoption of the ability to move by means of a more erect posture of the hindlimb.

4. *Procynosuchus autapomorphic characters*

The following characters of *Procynosuchus* are as yet unknown in any other cynodonts, or other therapsid group.

Broad, horizontal lumbar zygapophyses.
Antero-posteriorly elongated haemal arches.
Humerus relatively flat.
Radius and ulna with flat proximal ends (more distal parts of these bones unknown).
Bones of the manus very flat.
Wide, shallow acetabulum.
Deep flexor fossa on distal end of femur.
Tibia and fibula very flat, and fibula robust and straight.

All of these characters correlate directly with the swimming ability of *Procynosuchus*, and it is considered highly improbable that any of them are ancestral to the corresponding characters of the Triassic cynodonts.

5. *Synapomorphic characters of the Triassic cynodonts*

The characters that *Procynosuchus* had not evolved that were generally typical of all the later cynodonts include the following.

Accessory zygapophyseal articulations between the vertebrae.
Parapophyseal articulation for the ribs shared between adjacent centra.
Neural spines of the dorsal vertebrae very close to one another.
Reduced tail.
Ribs with expanded, overlapping costal plates at least in the posterior region. Rib cage shortened, owing to reduction of the rib shafts of all lumbar vertebrae.
Spinatus fossa on lateral face of the scapula.
More restrictive glenoid fossa.
Ilium more expanded anteriorly.
Pubo-ischiadic plate reduced.
Trochanter major enlarged.

These new characters reflect, at least in part, the loss of the ability to move in a sprawling gait, and the adoption of an obligatory rather than merely a facultative erect gait of the hindlimb.

The evolution of the later cynodont and ultimately mammalian pattern of locomotion occurred through a series of hypothetical intermediate forms. *Procynosuchus*, with its specializations for aquatic locomotion, cannot itself be considered one of these stages. Nevertheless, by recognition of the particular combination of plesiomorphic characters and later cynodont synapomorphic characters possessed by *Procynosuchus*, the nature of the hypothetical common ancestor of *Procynosuchus* and the Triassic cynodonts may be postulated.

These particular characters lead to the view that, like *Procynosuchus*, this hypothetical form had the ability to use its hind leg in either a sprawling gait or in an erect gait. The forelimb, by contrast, was capable only of a sprawling gait, but this was unimportant since the forelimb was not used to generate significant locomotory forces. Also, the lateral undulation of the vertebral column, a component of primitive tetrapod locomotion, had been largely abolished. It was compensated for by an increase in the locomotory force deriving from the rotation of the femur about its long axis.

The locomotion of the Triassic cynodonts, certainly the larger forms like *Diademodon* and *Cynognathus*, and the later traversodonts (Kemp 1980) appears to have changed, by the adoption of an obligatory erect gait of the hindlimb, and loss of the sprawling gait. Presumably, the possession of a dual-gait implies a compromise in the structure of the postcranial skeleton in terms of good design for either particular mode of locomotion. Loss of the sprawling gait may be seen, therefore, as a perfecting of the design for erect gait. The unique axial characters of the Triassic cynodonts, accessory zygapophyses, expanded ribs, etc., were probably devices to increase the rigidity of the vertebral column (Jenkins 1971), in relation to the habit of carrying the body permanently above the ground. The changes in the pelvis and hindlimb relate directly to the improved erect gait. It is interesting that the humerus of the later cynodonts appears still to have its movement restricted to a horizontal plane, suggesting that in them, as in *Procynosuchus*, it was the length of the stride alone, and not the production of locomotory forces, which was significant in forelimb design.

In conclusion, the evolutionary significance of the postcranial skeleton of *Procynosuchus* is that it supports the tentative hypothesis that I have proposed (Kemp 1978), that the intermediate locomotory pattern between primitive sprawling and the erect gait of mammals was a dual-gait, and not a single intermediate type of gait.

Once again, I should like to express my thanks to the Royal Society for a grant for the expedition to the Luangwa Valley, where this specimen was found, and to the Geological Survey of Zambia for their support.

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REFERENCES

Bakker, R. T. 1975 Experimental and fossil evidence for the evolution of tetrapod bioenergetics. In *Perspectives in biophysical ecology* (eds. D. Gates & R. Schmerl), pp. 365–399. New York: Springer-Verlag.

Bellairs, A. 1969 *The life of reptiles*. London: Weidenfeld & Nicolson.

Bonaparte, J. F. 1963 Descripción del esqueleto postcraneano de *Exaeretodon* (Cynodontia-Traversodontidae). *Acta geol. lilloana* **4**, 129–133.

Brink, A. S. 1951 Studies of Karroo reptiles. *S. Afr. J. Sci.* **47**, 338–347.

Brink, A. S. 1955 A study on the skeleton of *Diademodon*. *Palaeont. afr.* **3**, 3–39.

Brink, A. S. 1956 Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles. *Palaeont. afr.* **6**, 15–22.

Brink, A. S. & Kitching, J. W. 1953 On *Leavachia duvenhagei* and some other procynosuchids in the Rubidge collection. *S. Afr. J. Sci.* **49**, 313–317.

Broom, R. 1948 A contribution to our knowledge of the vertebrates of the Karroo Beds of South Africa. *Trans. R. Soc. Edinb.* **61**, 577–629.

Cox, C. B. 1959 On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proc. zool. Soc. Lond.* **132**, 321–367.

Gregory, W. K. 1912 Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. *Ann. N.Y. Acad. Sci.* **22**, 267–294.

Gregory, W. K. & Camp, C. L. 1918 Studies in comparative myology and osteology. No III. *Bull. Am. Mus. nat. Hist.* **38**, 447–563.

Hopson, J. A. & Kitching, J. W. 1972 A revised classification of cynodonts (Reptilia; Therapsida). *Palaeont. afr.* **14**, 71–85.

Jayes, A. S. & Alexander, R. McN. 1978 Mechanics of locomotion of dogs (*Canis familiaris*) and sheep (*Ovis aries*). *J. Zool.* **185**, 289–308.

Jenkins, Jr., F. A. 1971 The postcranial skeleton of African cynodonts. *Bull. Peabody Mus. nat. Hist.* no. 36, pp. 1–126.

Jenkins, Jr., F. A. 1973 The functional anatomy and evolution of the mammalian humero-ulnar articulation. *Am. J. Anat.* **137**, 281–298.

Jenkins, Jr., F. A. 1974 The movement of the shoulder in claviculate and aclaviculate mammals. *J. Morph.* **144**, 71–84.

Kemp, T. S. 1969 The atlas–axis complex of the mammal-like reptiles. *J. Zool.* **159**, 223–248.

Kemp, T. S. 1975 Vertebrate localities in the Karroo System of the Luangwa Valley, Zambia. *Nature, Lond.* **254**, 415–416.

Kemp, T. S. 1978 Stance and gait in the hindlimb of a therocephalian mammal-like reptile. *J. Zool.* **186**, 143–161.

Kemp, T. S. 1979 The primitive cynodont *Procynosuchus*: functional morphology of the skull and relationships. *Phil. Trans. R. Soc.* B **285**, 73–122.

Kemp, T. S. 1980 Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *J. Zool.* (In press)

Konjukova, E. D. 1946 New data on *Permocynodon sushkini* Woodward, the cynodont from the North Dvina fauna. *Dokl. Akad. Nauk SSSR* **54**, 527–530.

Manter, J. T. 1938 The dynamics of quadrupedal walking. *J. exp. Biol.* **15**, 522–540.

Parrington, F. R. 1961 The evolution of the mammalian femur. *Proc. zool. Soc. Lond.* **137**, 285–298.

Romer, A. S. 1922 The locomotor apparatus of certain primitive and mammal-like reptiles. *Bull. Am. Mus. nat. Hist.* **46**, 517–606.

Romer, A. S. & Price, L. W. 1940 Review of the Pelycosauria. *Spec. Pap. geol. Soc. Am.* **28**, 1–538.

Tarasoff, F. J., Pierard, A. B. J. & Whitt, A. P. 1972 Locomotory patterns and external morphology of the river otter, sea otter, and harp seal (Mammalia). *Can. J. Zool.* **50**, 915–929.

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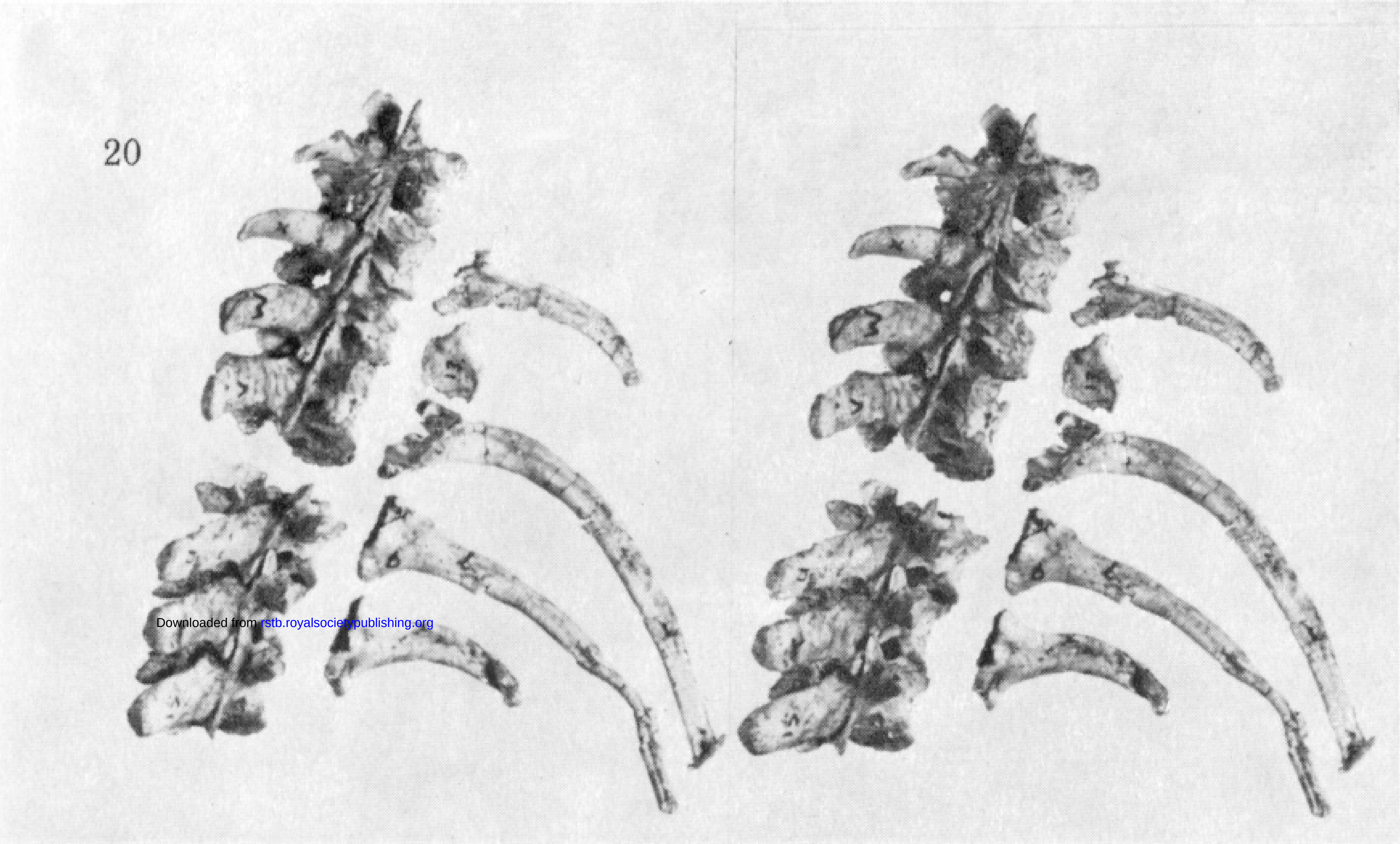

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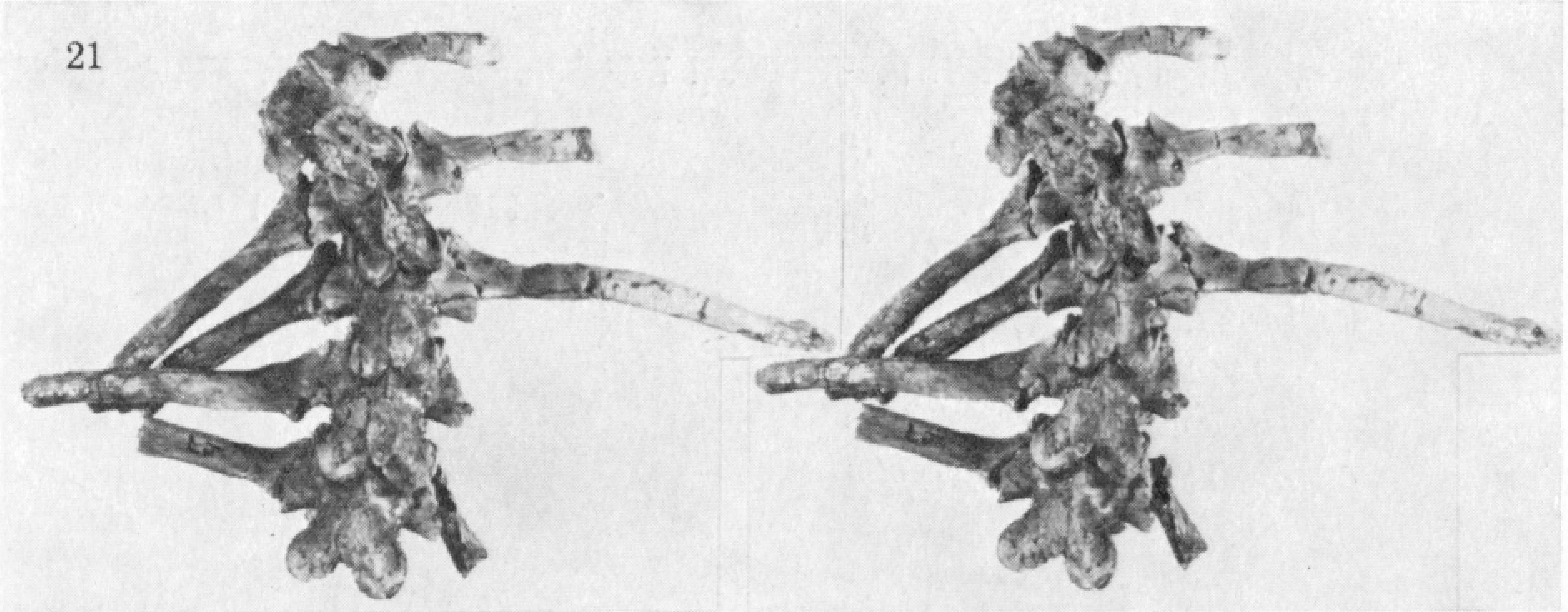

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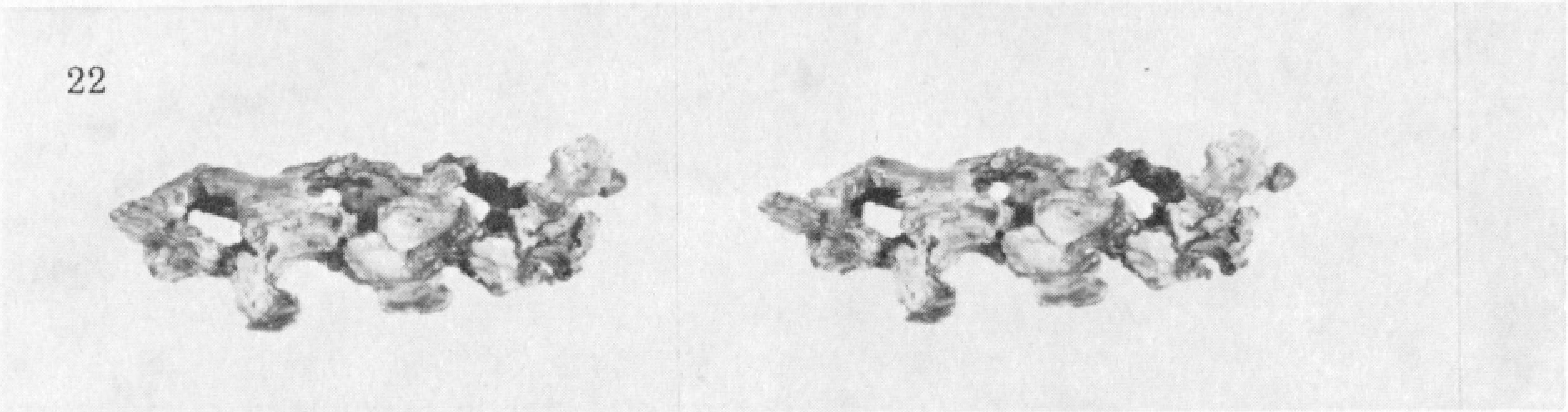

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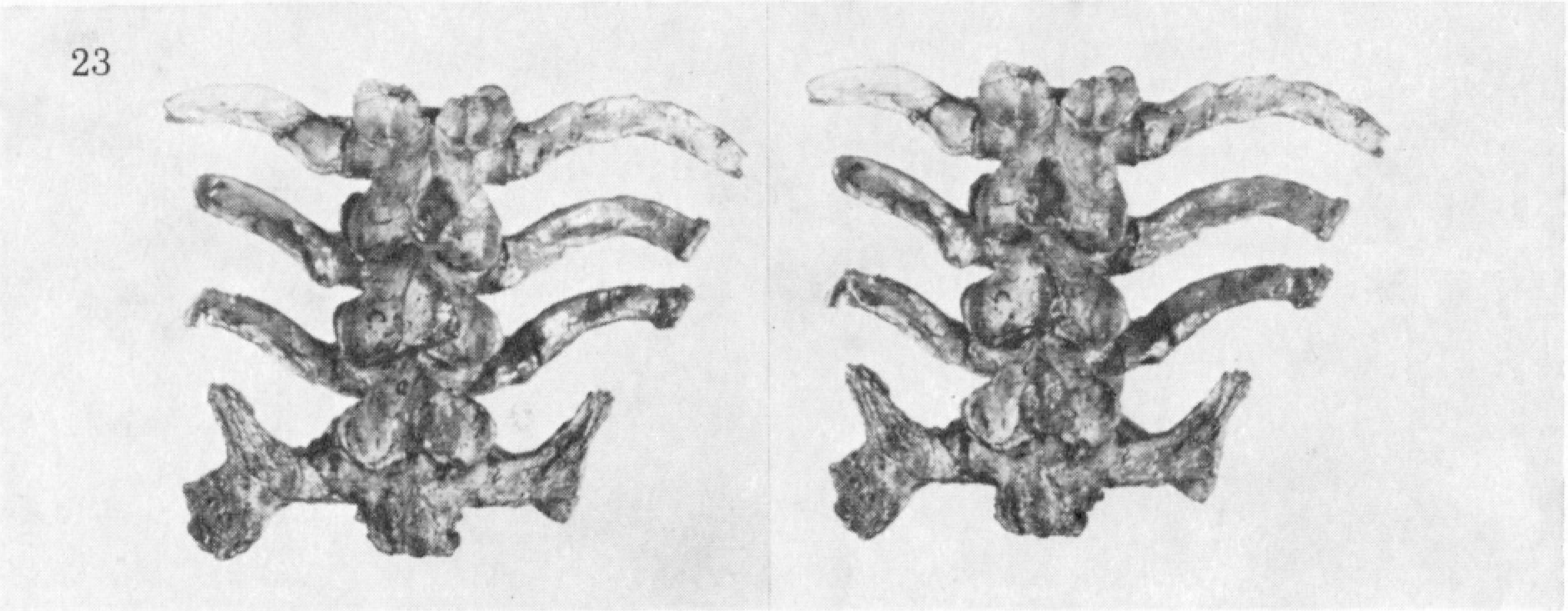

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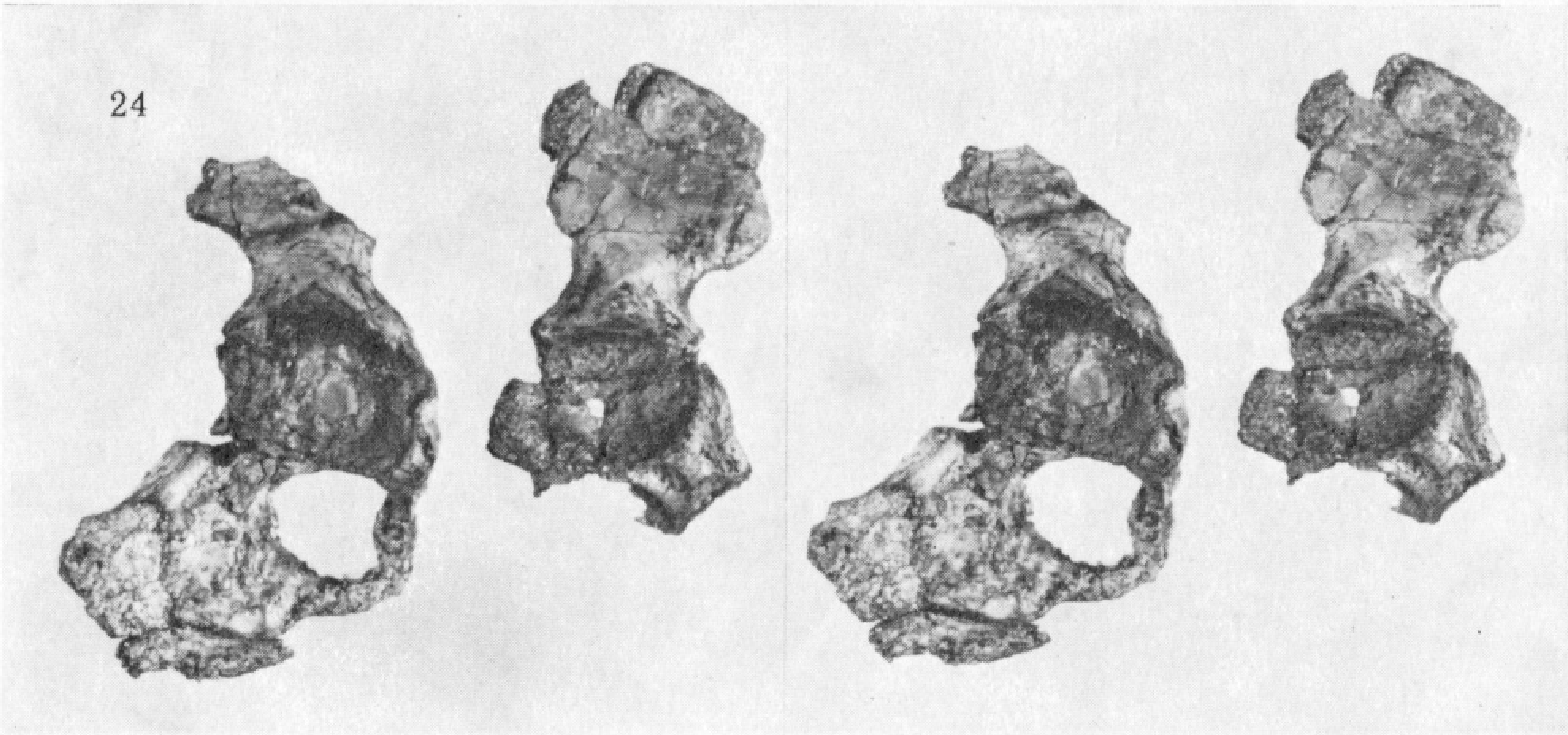

FIGURE 20. Vertebrae 5 to 11, with right ribs 6 to 10. Two-thirds natural size.
FIGURE 21. Vertebrae 16 to 20. Two-thirds natural size.
FIGURE 22. Caudal vertebrae, with haemal arches. Natural size.
FIGURE 23. Vertebrae 26 to 28, and first sacral vertebra. Two-thirds natural size.
FIGURE 24. Right and left pelvic girdles in lateral view. Two-thirds natural size.

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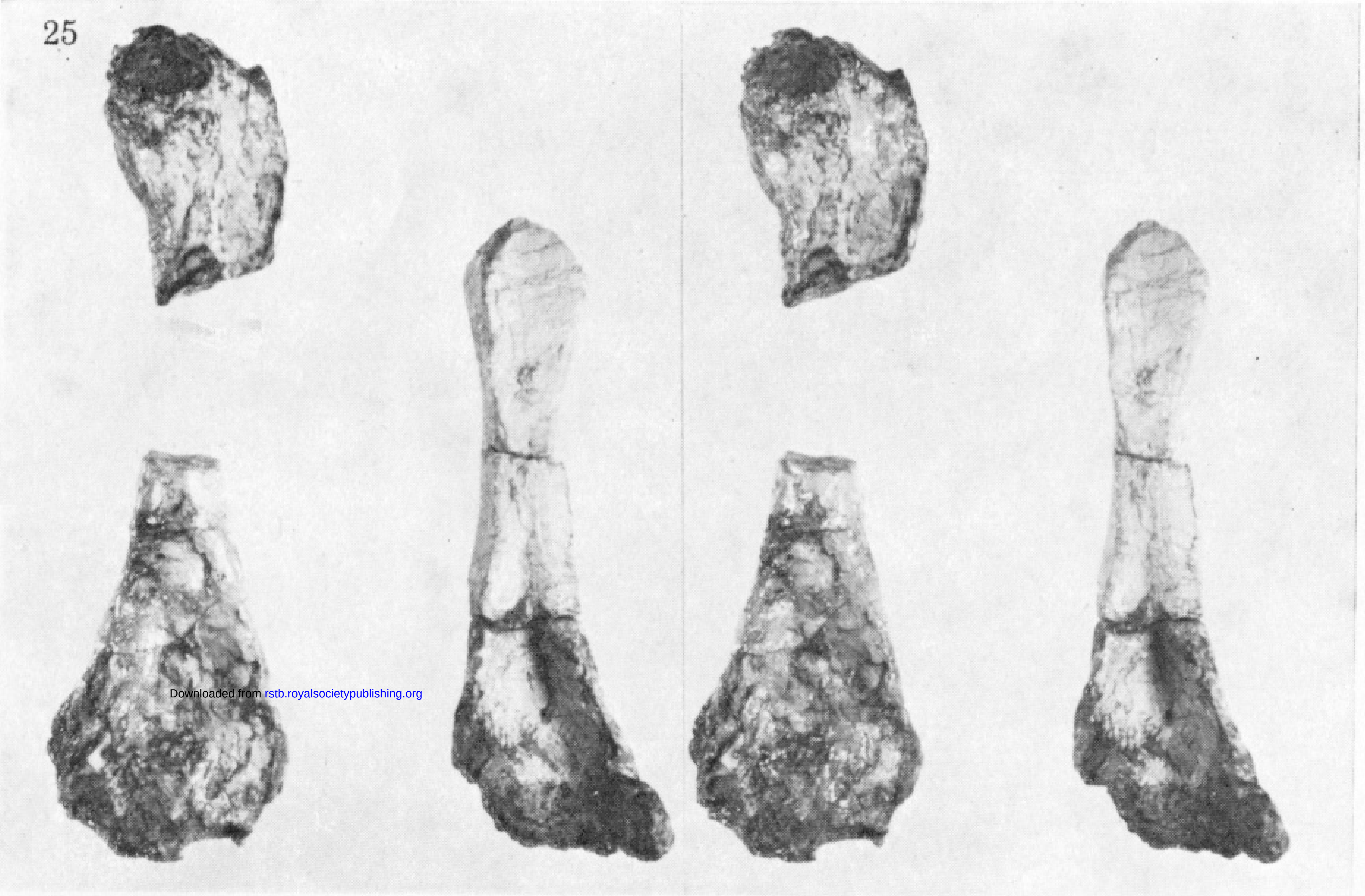

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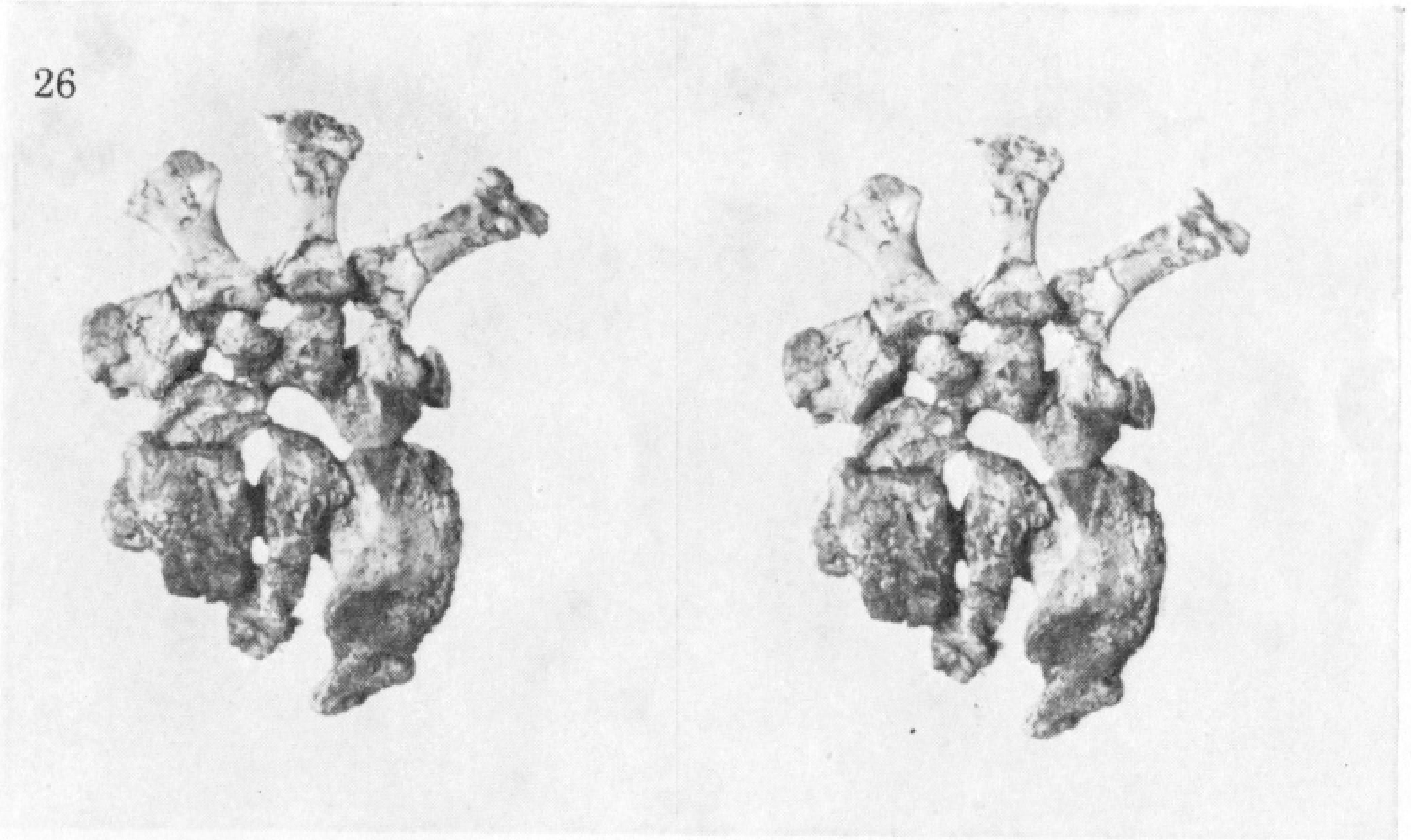
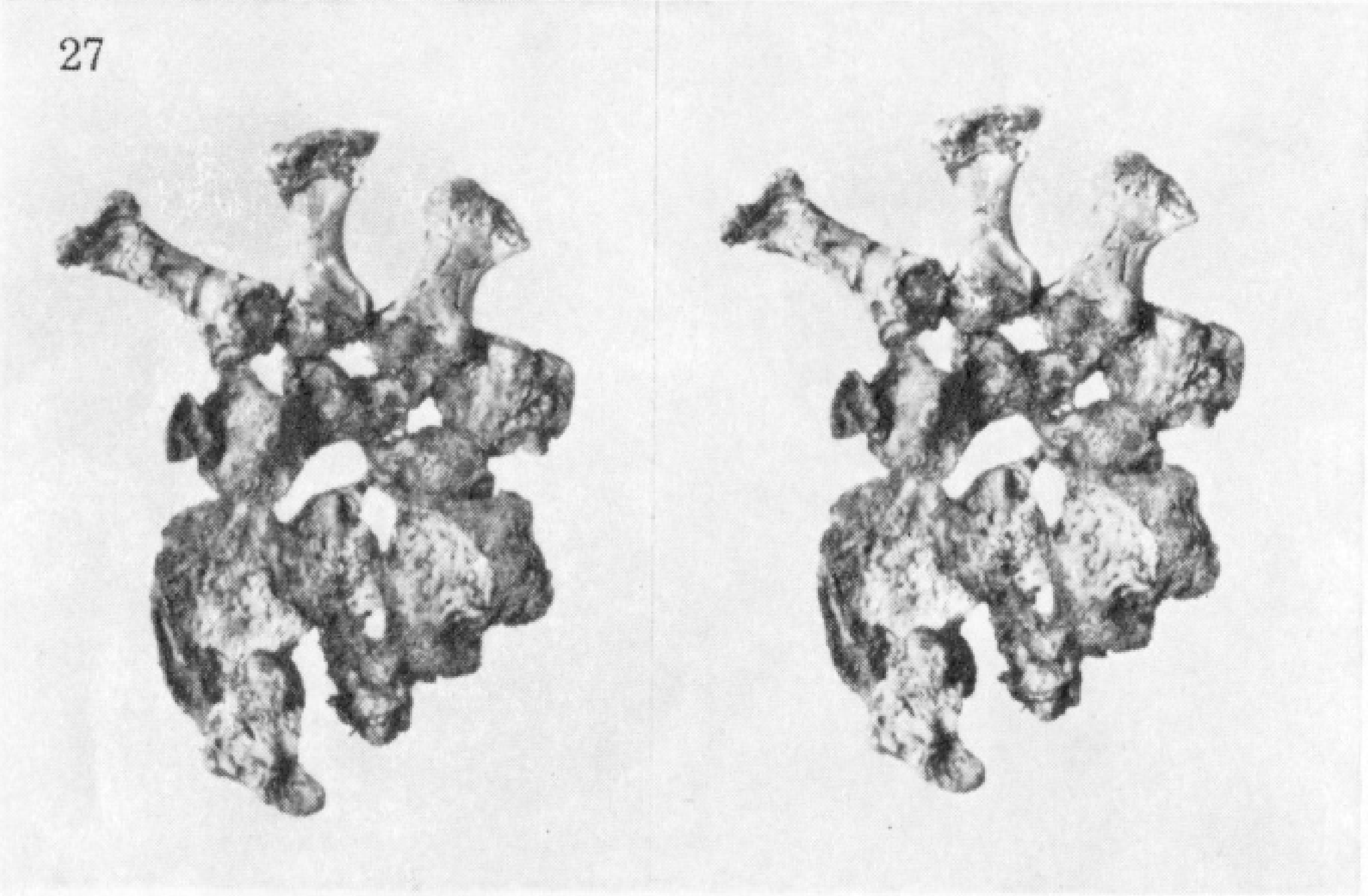


27



28

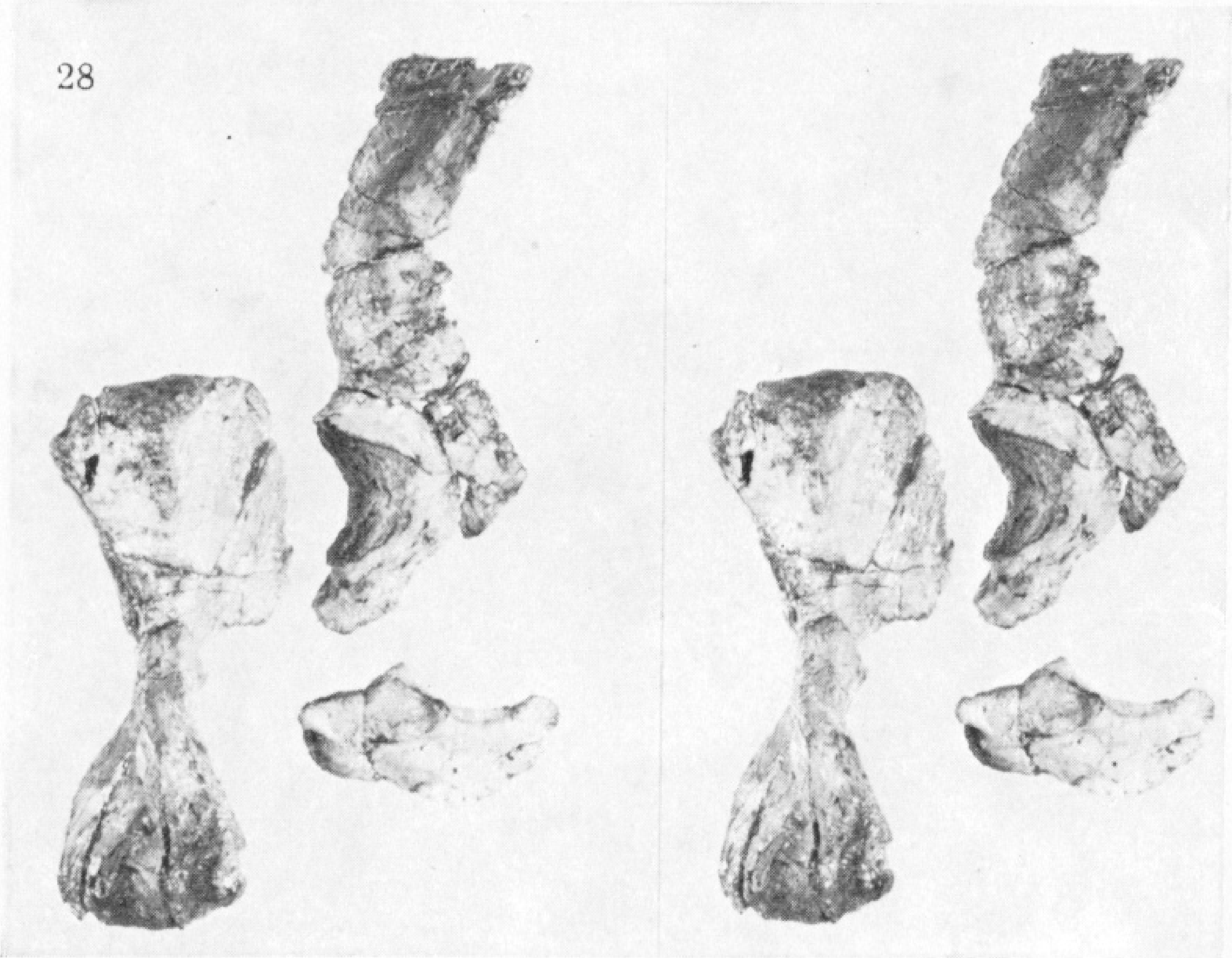


FIGURE 25. Right femur in dorsal view, and left femur in ventral view. Natural size.

FIGURE 26. Right manus in dorsal view. Natural size.

FIGURE 27. Right manus in ventral view. Natural size.

FIGURE 28. Right humerus in dorsal view, right scapulo-coracoid in lateral view, and left coracoid in lateral view. Two-thirds natural size.