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THE SKELETON OF A BAURIOID THEROCEPHALIAN THERAPSID FROM THE LOWER TRIASSIC (*LYSTROSAURUS* ZONE) OF SOUTH AFRICA

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ABSTRACT—On the basis of a single, virtually complete specimen of a baurioid ("scaloposaur") therocephalian, the first full reconstruction of a member of this group is given. It shows that these therapsids were very mammal-like in their proportions, with relatively long limbs, attenuated lumbar ribs, and a highly reduced tail. The specimen is referred to Regisauridae, indet.

The degree of differentiation of the axial skeleton is similar to that found in cynodont therapsids, although the head was probably capable of less dorso-ventral movement at the occipito-atlas joint, and there is evidence for a greater degree of lateral undulation of the trunk in the lumbar region. The shoulder girdle was probably highly mobile. The structure of the pelvis and hindlimb supports the hypothesis that the primitive therapsid hindlimb could operate in either a sprawling mode, or in a more advanced, parasagittal mode facultatively.

The lack of periosteal bone over the ends of the centra and other bones, and the open nature of the sutures between the centra and neural arches, and between the centra and the lumbar and sacral ribs, support the view that 'scaloposaurs' such as this were immature specimens.

INTRODUCTION

This study concerns a virtually complete specimen of a small therocephalian therapsid, of the kind usually referred to as the scaloposaurs, from the Lower Triassic *Lystrosaurus* zone of South Africa.

The Therocephalia form one of the major carnivorous therapsid groups (Kemp, 1982). Specimens are known from Upper Permian deposits of southern Africa and also from the Zone IV Permian of Russia. A small number of lineages survived the Permo–Triassic boundary to appear in the Lower Triassic, particularly the *Lystrosaurus* zone, and one family, the Bauriidae, occurs in the younger *Cynognathus* zone. Related Lower Triassic forms have been found at localities in Russia (Tatarinov, 1974) and China (Sigogneau-Russell and Sun, 1981; Sun and Ho, 1981; Li, 1984).

Systematically, the Therocephalia is generally accepted as the sister group of the Cynodontia, the more advanced therapsid group that dominated the mammal-like reptile faunas during the Triassic, and which are the closest relatives of the mammals (Kemp, 1972, 1982; Hopson and Barghusen, in press). The interrelationships within the group are less confidently understood. Hopson and Barghusen (in press) have attempted a cladistic analysis, in which they recognise an advanced monophyletic group Baurioidea, including the Triassic forms and also certain Late Permian genera. It also includes the series of small forms formerly referred to as the Scaloposauria, which are characteristically only a few inches in length and have a reduced postorbital bar. Hopson and Barghusen have abandoned the taxon Scaloposauria, however, on the grounds that it includes the juvenile forms of a range of therocephalians, mainly but not exclusively baurioids, which have little in common other than small size and other features, such as the reduced postorbital bar, relatively wide intertemporal region, and small canines, which they believe to be associated only with immaturity.

The present specimen is just such a form, being only about 17 cm in presacral length. Given that it may be a juvenile of one of several different genera, its identification is difficult because it lacks the anterior part of the skull, and therefore the most critical region for generic identification, the details of the anterior part of the palate (Mendrez, 1975; Mendrez-Carroll, 1979; Hopson and Barghusen, in press). Dr. J. A. Hopson (pers. comm.) has suggested that the specimen is a juvenile *Regisaurus* (Mendrez, 1972). The arrangement of the bones in the posterior region of the internal nares is very like that in *Regisaurus*, with the vomer gradually widening anteriorly, almost contacting the maxilla at the anteriormost part of the skull as preserved. However, the specimen also possesses a small parietal foramen, absent in *Regisaurus*. Probably the best identification at present for this specimen is Regisauridae indet.

The major interest of the specimen is its exceptionally complete and well preserved postcranial skeleton. The complete skeletons of few therapsids have been described, and that of the Therocephalia is the least well known of all. Watson (1931) described and attempted a reconstruction of the baurioid *Ericiolacerta*, but the material was incomplete and poorly preserved
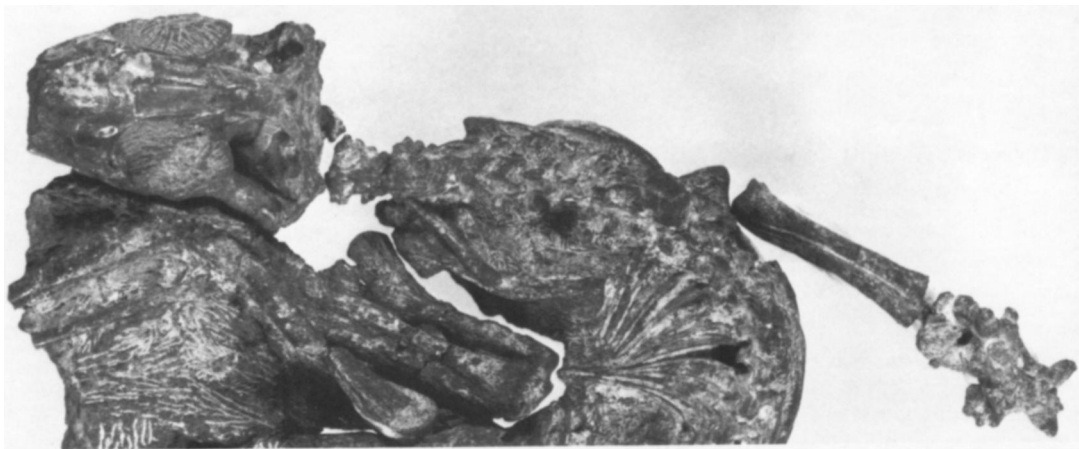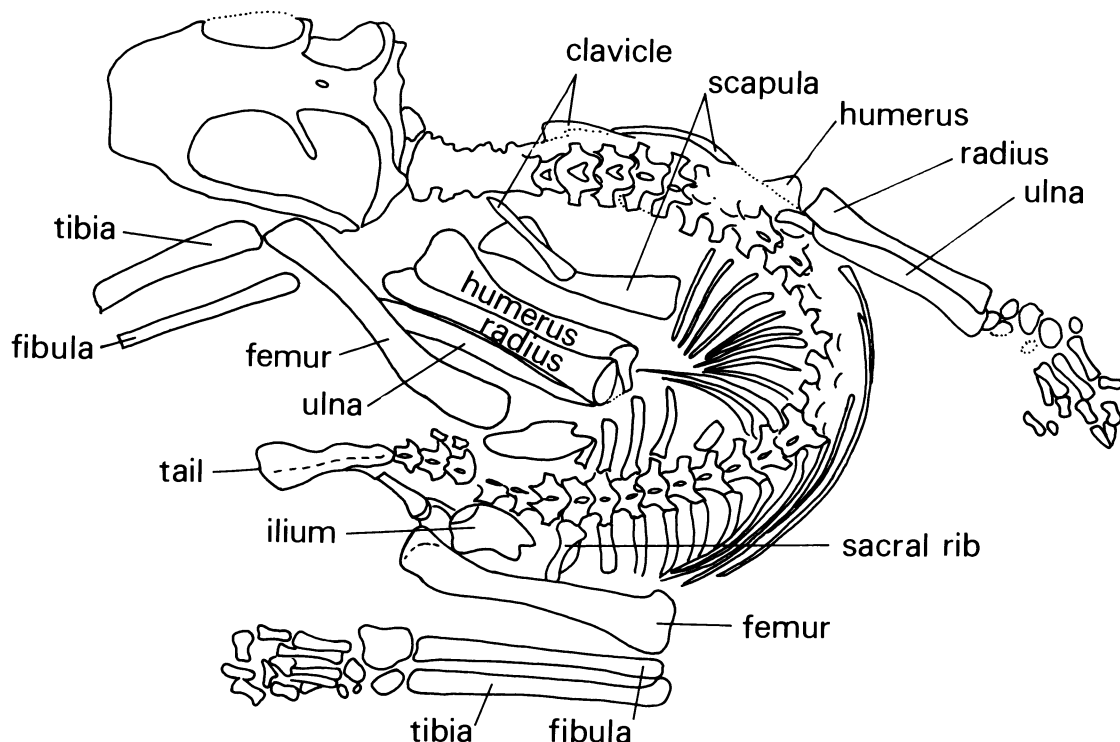
FIGURE 1. Regisauridae, indet. Left, stereophotographs of the anterior and the posterior parts of the skeleton. Right, diagrammatic representation of skeleton. Magnification ×1.

in several respects. Brink (1956a) illustrated the skeleton of a juvenile whaitsiid referred to *Aneugomphius*, but this is actually a poor specimen, with very little detail satisfactorily exposed. Attridge (1956) and Cys (1971) described the skeleton of the peculiar therocephalian *Mirotenthes*, and Cys (1967) described a complete specimen of the pristerognathid *Cynariognathus*. For the rest, the therocephalian skeleton is known only from descriptions of fragmentary material, such as those of Boonstra (1964) on the limbs and girdles of pristerognathids; Brink (1965) on the anterior skeleton of *Olivieria*; Sigogneau (1963) on the anterior part of the skeleton of the "scaloposaur" *Tetracynodon*; Kemp (1978) on the pelvis and hindlimb of *Regisaurus*.

MATERIAL

Specimen—Cambridge University Museum of Zoology T837. Measurements given in Table 1.

Locality—Harrismith, northeastern Orange Free State, South Africa.

Horizon—*Lystrosaurus* zone, Lower Triassic. Collected by F. R. Parrington.

The specimen (Fig. 1) is complete except for the anterior half of the preorbital region of the skull, the distal half of the left tibia and fibula, the left pes and left manus, and some of the phalanges of the right pes and manus. The skeleton is articulated, and preserved in a curved orientation. A small amount of disarticulation of the shoulder girdle bones and the pelvis has occurred.

The matrix is a characteristically hard, red *Lystrosaurus* zone mudstone, with a small amount of crystallization here and there. Preparation has been entirely by mechanical means.

SKULL

The skull (Fig. 2) is practically undistorted and complete except for the zygomatic arches and the anterior half of the snout. The pattern of bones is as shown on the figures, and is very similar to that of other baurioid therocephalians such as *Scaloposaurus* (Mendrez-Carroll, 1979) and *Regisaurus* (Mendrez, 1972). Attention will only be paid to points of particular interest.

A rather unusual feature is the manner in which the nasal, prefrontal, lachrymal, and maxillary bones meet

TABLE 1. Dimensions (mm).

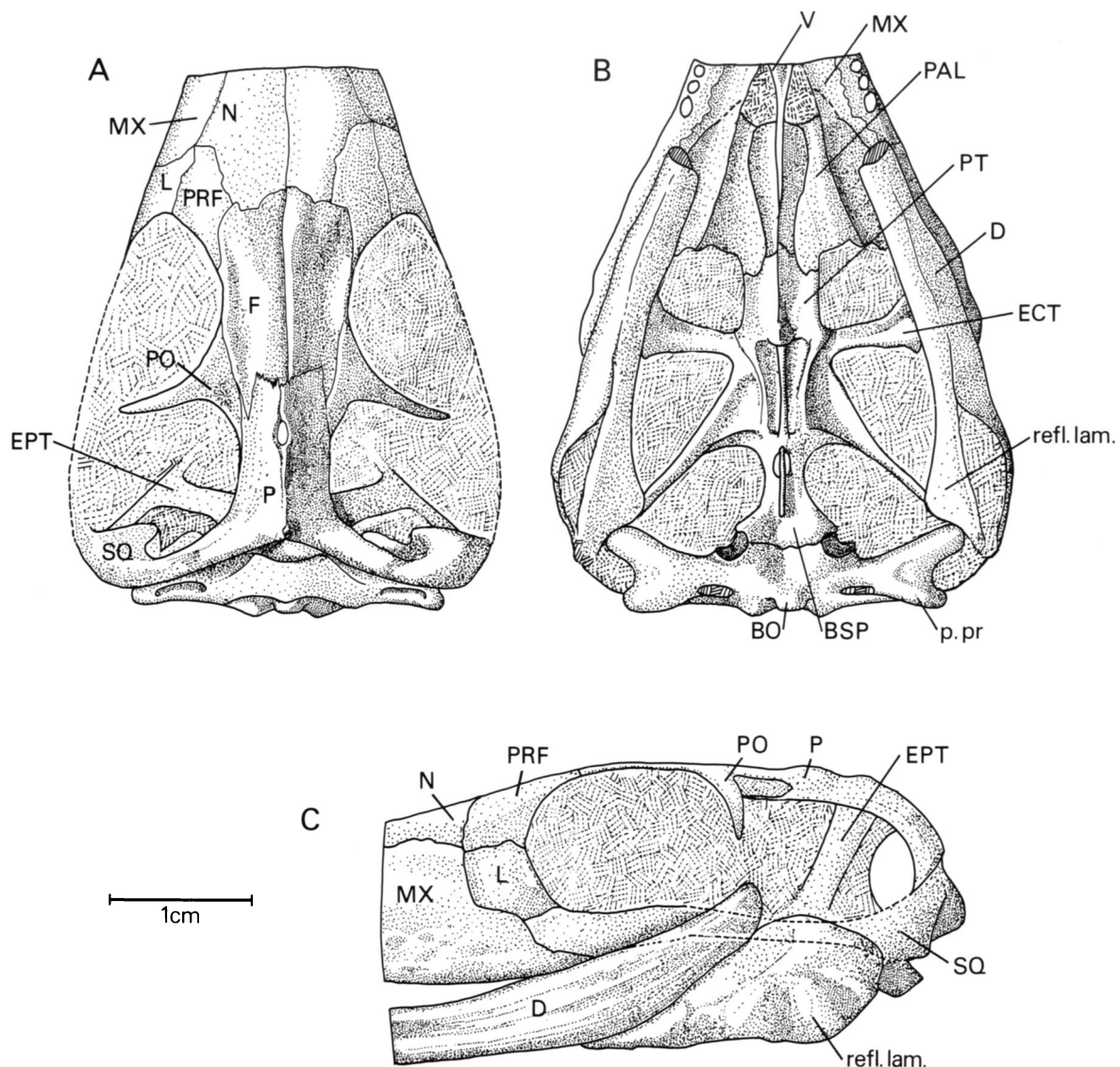|	
Skull (estimated)	51
Presacral vertebrae	116
Postsacral tail	25
Humerus	32
Radius	29
Ulna	29
Manus (estimated)	27
Femur	38
Tibia	38
Fibula	33
Pes (estimated)	33

FIGURE 2. Regisauridae, indet. Skull reconstruction. **A**, dorsal view; **B**, ventral view; **C**, lateral view. Magnification ×2. Abbreviations: **BO**, basioccipital; **BSP**, basisphenoid; **D**, dentary; **ECT**, ectopterygoid; **EPT**, epipterygoid; **F**, frontal; **L**, lachrymal; **MX**, maxilla; **N**, nasal; **P**, parietal; **PAL**, palatine; **PO**, postorbital; **p.pr**, paroccipital process; **PRF**, prefrontal; **PT**, pterygoid; **refl.lam.**, reflected lamina of the angular; **SQ**, squamosal; **V**, vomer.

almost at a single point. In therocephalians in general the maxilla and prefrontal meet, excluding any contact of the nasal with the lachrymal; in cynodonts the reverse is true.

The postorbital bar is incomplete on both sides, a characteristic of "scaloposaurs", but because the zygomatic arches are missing, it is possible that there was a connection between the postorbital bar and the arch in life.

A small parietal foramen is present, which is the most obvious distinction between this skull and the *Regisaurus* described by Mendrez (1972). However, the possibility of closure of a parietal foramen during juvenile growth cannot be excluded.

The palate, which is critical for identification of bau-

rioids (Mendrez, 1975; Hopson and Barghusen, in press) unfortunately lacks the anterior part, and therefore the extent of development of a secondary palate is unknown. The palatal surface is only shallowly vaulted, forming a low choanal passage, and the vomer widens almost to contact the medial edges of the maxillae at the anteriormost part of the preserved structure. Thus, as far as it is possible to say, the palate resembles that of *Regisaurus*. Certainly the palate was not as well developed as in *Ericiolacerta* and *Lycideops*, but was probably more progressive than in *Ictidosuchoides* (Mendrez, 1975).

Remnants of a series of orbital sclerites are preserved within the right temporal fenestra.

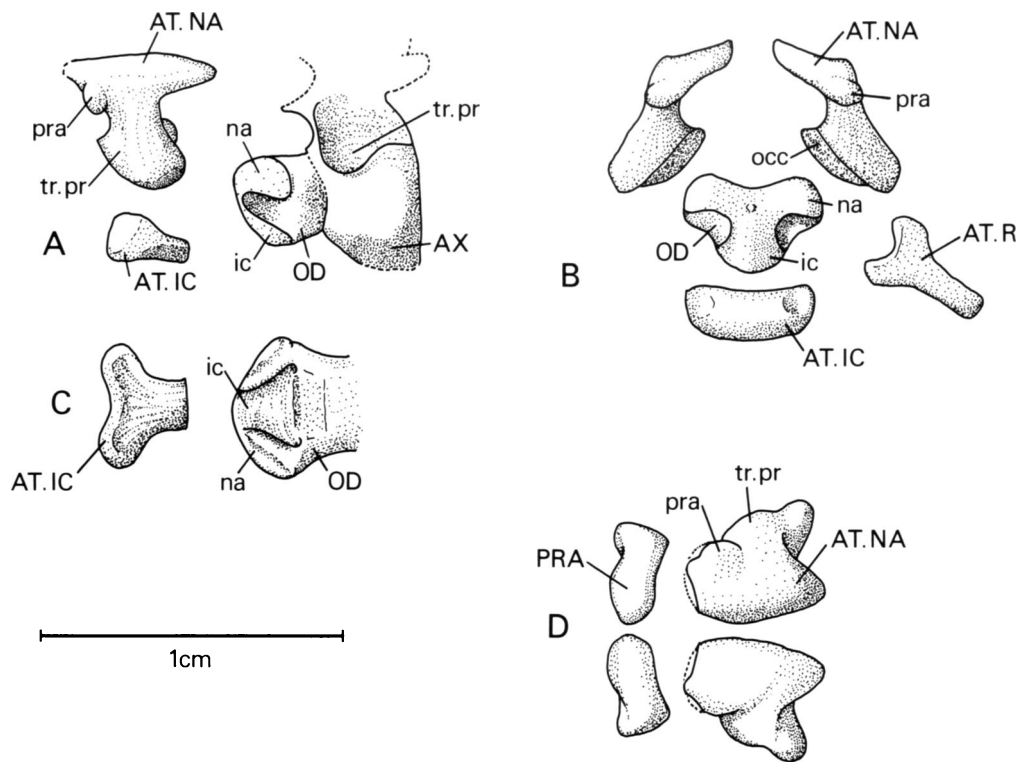The dentition is very poorly preserved. Only one

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FIGURE 3. Regisauridae, indet. Atlas-axis complex. **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Magnification ×4. Abbreviations: **AT.IC**, atlas intercentrum; **AT.NA**, atlas neural arch; **AT.R**, atlas rib; **AX**, axis; **ic**, facet for atlas intercentrum; **na**, facet for atlas neural arch; **occ**, facet for occipital condyle; **OD**, odontoid (atlas centrum); **PRA**, proatlas; **pra**, facet for proatlas; **tr.pr**, transverse process.

tooth, a relatively young, unworn postcanine still has the crown. It shows a small anterior accessory cusp and an almost imperceptible posterior accessory cusp, rather similar to those of *Scaloposaurus* (Mendrez-Carroll, 1979). The postcanine teeth of *Regisaurus* (Mendrez, 1972) appear to be simple cones, although they are not yet adequately known.

THE AXIAL SKELETON

Vertebral Column (Fig. 10)—This is complete from the atlas to the tip of the tail, and has been prepared from the dorsal side only, although representative individual vertebrae have been prepared more completely to show the full structure. Twenty-seven presacral vertebrae are present including the atlas and the axis, which is the normal number for therapsids. Three sacral vertebrae are followed by a very reduced caudal series of nine, or possibly ten, vertebrae that rapidly attenuate in size. The presacral regions of the column are less differentiated than in mammals, but there is a general distinction between about seven cervical vertebrae, fourteen or fifteen thoracic vertebrae, and five or six lumbar vertebrae. This is closely comparable to the situation in cynodonts (Jenkins, 1971a; Kemp, 1980a).

The individual vertebrae are simple, lacking the ac-

cessory articulations of all but the most primitive cynodonts (Kemp, 1980a; certain advanced cynodonts also lack them, e.g. Jenkins, 1970). There is a persistent suture between the neural arch and the centrum throughout the column. Indeed, the upper parts of the centra are incompletely ossified and lack a periosteal layer, which probably indicates immaturity (see page 228). The centrum of the fifth cervical vertebra has conveniently shifted out of place allowing it to be fully prepared. It demonstrates the deep amphicoely characteristic of other therapsids and there is a marked mid-dorsal pit penetrating the centrum, a feature that also occurs in gorgonopsids (pers. obs.).

Atlas-axis Complex (Fig. 3)—The first two vertebrae are strikingly similar to those of cynodonts (Kemp, 1969, 1980a; Jenkins, 1971a). A pair of flat, leaf-like proatlantes (Fig. 3D) are present, lying on top of the atlas neural arches. Each atlas neural arch consists of a flat dorsal component lying almost horizontally and bearing a small boss for the proatlas on its anterior edge. The transverse process forms a sharp angle with the dorsal component, and extends ventro-laterally. The more distal part is expanded both antero-posteriorly and medially, and this part bears a flat, oval facet for articulation with the occipital condyle (Fig. 3B). The facet of the atlas neural arch that articulates with the odontoid is not exposed. The posteriormost part

of the atlas neural arch consists of a blunt point that represents the postzygapophysis.

The atlas intercentrum has been displaced ventrally so that most of its structure is revealed. In anterior view (Fig. 3B) it is kidney shaped, and almost the entire surface is occupied by a slightly concave facet for the lower part of the occipital condyle. The antero-lateral part is expanded as a parapophysis (Fig. 3C). Behind the parapophyses, the bone is narrower both transversely and dorso-ventrally, and its dorsal surface consists of a longitudinally aligned, shallow trough that matches the ventral facet of the odontoid.

The odontoid, or atlas centrum, is not fused either laterally or ventrally to the axis centrum behind; the dorsal contact between these two bones is not exposed. As in cynodonts, the odontoid has three distinct articulating facets, which meet centrally at a very slight swelling (Fig. 3B). The paired dorso-lateral facets are slightly convex and articulate with the pair of atlas neural arches, while the broader mid-ventral facet faces forwards and downwards. It is convex from side to side and linear from front to back, and matches the facet of the atlas intercentrum.

An atlas rib is preserved although only exposed in anterior view (Fig. 3B). It is very small, with a double head from which a narrow, parallel-sided shaft extends.

The axis vertebra (Fig. 3A) is rather poorly preserved, lacking the neural spine and the ribs. The centrum is tightly attached to the atlas centrum. The axis intercentrum has been partially displaced and damaged. The axis transverse process is very short and inclined ventro-laterally, approximately parallel to the atlas transverse process. The prezygapophyses are damaged and the postzygapophyses are not well preserved. The latter appear to be broad, with articulating surfaces close to horizontal, very like those of the succeeding cervical postzygapophyses.

Cervical Vertebrae and Ribs (Fig. 4A, D, E)—The third to the sixth vertebrae are characterised by broad zygapophyses bearing more or less horizontal articulating surfaces. The transverse processes are short, stout and lie well down on the neural arches, almost at the level of the suture with the centrum. A definite angulation separates the main part of the neural arch from the transverse process. The neural spines have all broken off, but they appear to have been relatively robust. The poor ossification of the ends of the centra prevent recognition of parapophysial facets, and similarly there is no evidence of the presence of intercentra, although they could have occurred in an unossified state. The seventh vertebra has cervical-like prezygapophyses, but the postzygapophyseal width is reduced, and it is therefore morphologically transitional to the thoracic vertebrae, much like the condition of the seventh cervical vertebra of the cynodont *Thrinaxodon* (Jenkins, 1971a).

The ribs of vertebra three are missing. The right rib of vertebra four is almost completely obscured, but those of the remaining cervical vertebrae are well ex-

posed. The fifth rib (Fig. 4D) is short, slender and slightly curved, with a prominently dichotomous head. The dorsal head is slightly thicker than the ventral head. The sixth rib (Fig. 4E) is longer and the dorsal head is even more prominent than the ventral head. Rib seven continues the trend of increasing length, but unfortunately its head is not exposed. All of these cervical ribs are partly displaced and therefore their exact orientation in life is indeterminate.

Thoracic Vertebrae and Ribs (Fig. 4B, F, G)—The thoracic vertebrae (Fig. 4B) are characterised by narrow zygapophyses, with their articulating surfaces at about 60° to the horizontal. The transition to this arrangement from the cervical vertebrae is completed by vertebra nine. The thoracic neural spines are relatively thin and inclined slightly backwards. The transverse processes are particularly distinctive, being discretely set off from the neural arch, parallel sided, and extending laterally. They remain high up on the neural arch, around the level of the zygapophyses, and the distal ends are slightly upturned. A ventral buttress connects the front edge of the transverse process to the neural arch, while a similar but less prominent ridge connects the hind edge to the arch. Therefore the underside of both the transverse process and the adjacent part of the neural arch is concave. The centra of the thoracic vertebrae do not differ significantly from those of the cervical vertebrae. Again, poor ossification has made the parapophyses indistinct.

The two heads of the thoracic ribs (Fig. 4F, G) are confluent and there is a prominent ridge extending from the head region along the dorsal edge of the rib shaft. The proximal one-third of the shaft has a smoothly continuous curvature, followed by a long almost straight section. The distal one-quarter or so is then strongly recurved, at least in those ribs that have been fully exposed (Fig. 10).

Lumbar Vertebrae and Ribs (Fig. 4C)—The transition from thoracic to lumbar vertebrae occurs between vertebra twenty-one, which has slightly widened postzygapophyses, and vertebra twenty-three. The lumbar vertebrae have wide zygapophyses, reflecting articulating surfaces that lie at about 45° to the horizontal. The neural spines are a little longer antero-posteriorly, but have about the same height as in the thoracic vertebrae. The most prominent difference concerns the transverse processes, which extend antero-laterally rather than laterally, are positioned more ventrally on the neural arch, and have a generally more robust appearance. The diapophysis faces antero-laterally. The centrum, although not increased in overall size, has expanded along the dorso-lateral edge where it is in contact with the neural arch, giving an apparently stronger attachment between these two parts. Nevertheless, there is still no synostosis between centrum and arch.

The ribs of the lumbar region are particularly distinctive (Fig. 4C). The head is single, expands ventrally and antero-posteriorly, and is in tight contact with the
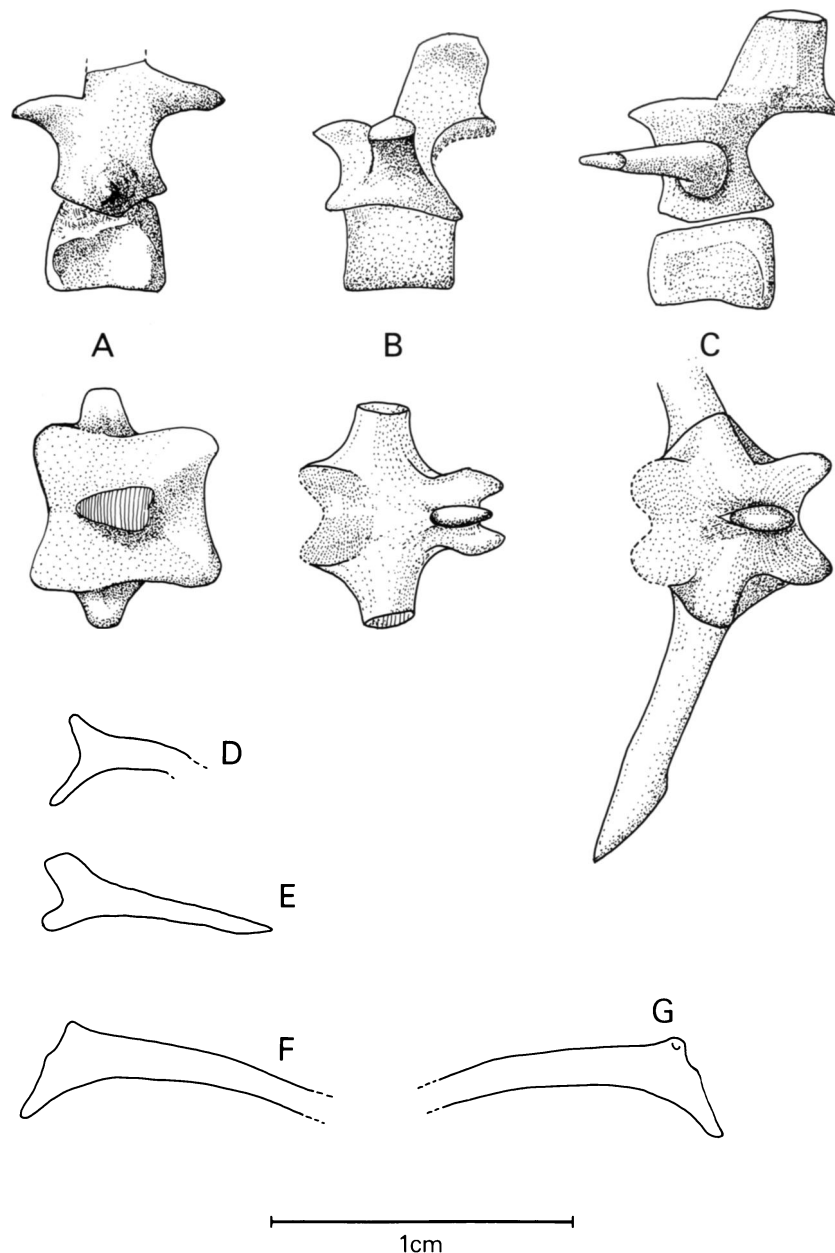
FIGURE 4. Regisauridae, indet. Vertebrae and ribs. **A**, cervical vertebra (fourth presacral); **B**, thoracic vertebra (fourteenth presacral); **C**, lumbar vertebra (twenty-sixth presacral). **D**, fifth rib in anterior view; **E**, sixth rib in anterior view; **F**, eighteenth rib in anterior view; **G**, seventeenth rib in posterior view. Magnification ×4.

diapophysis. No movement appears to have been possible between the rib and its vertebra. The shaft of the rib is oriented horizontally and extends antero-laterally from the head. The three posteriormost lumbar ribs are flattened dorso-laterally and are more or less straight. Further forwards, the lumbar ribs show a gradation to the form of the thoracic ribs, by becoming increasingly long and developing an increasing posterior and ventral curvature (Fig. 10). By vertebra twenty-one, the rib is essentially a short version of the more anterior thoracic ribs.

Sacrum (Fig. 10)—There are three sacral vertebrae, which have normal, lumbar-like zygapophyseal articulations with one another. Indeed, the first sacral vertebra is very lumbar-like in size and form, and the second and third sacrals differ only in their relatively smaller size. The first pair of lumbar ribs have been displaced forwards post mortem, indicating that they were not synostosed to the vertebrae. The facet on the first sacral vertebra for the rib head has been exposed; it occupies the whole of the distal face of the transverse process and extends onto the antero-dorsal region of

the centrum. Together, these parts form a continuous synapophysis of considerable dorso-ventral extent.

The head of the first sacral rib is expanded to fit the synapophysis. The short, stout shaft curves slightly ventrally and has an expanded distal end that contacts the ilium. Although they are not well exposed, the second two sacral ribs appear to be similar but smaller in all proportions.

Caudal Vertebrae (Fig. 10)—The tail is completely preserved, so there is no doubt about its very short length. There are nine caudal vertebrae, with the possibility of a tenth, vestigial one at the tip. Free, but very short, ribs are associated with the anterior three. No haemal arches are present, although it remains possible that such arches occurred on the more anterior caudal vertebrae, the ventral sides of which are obscured by the pelvis.

SHOULDER GIRDLE AND FORELIMB

The shoulder girdle is practically complete although it has only been possible to prepare the external surfaces of the bones. A large part of the interclavicle and all of the left procoracoid are obscured by overlying bones, and the individual elements are slightly displaced from one another. The right forelimb is complete except for some of the manus bones; the left humerus, radius, and ulna are also complete, but the left manus is absent, or possibly still present deep within the matrix.

Scapulo-coracoid (Fig. 5A, B, D)—The scapula is a remarkably slender bone that curves gently around the contour of the thoracic region of the body. At the same time, when it is oriented as in the reconstruction (Fig. 10), it curves forwards. The dorsal edge is sharp, almost straight, and offers no direct evidence for the existence of a cartilaginous suprascapula in life. Neither is there any apparent cleithrum, as described in *Ericiolacerta* by Watson (1931). The external surface of the dorsal region of the scapula is smooth, and very slightly convex from front to back. Both the anterior and the posterior edges are fairly sharp. On passing ventrally, the bone gradually constricts, and also thickens, so that the middle region of the scapula is quite rod-like. It is approximately semi-circular in cross section, with a continuously convex anterior, lateral, and posterior faces, and as far as can be seen, a flat internal face. The lower part of the scapula widens fairly rapidly, resulting in a broad, very slightly concave lateral face. The anterior part tapers to a sharp edge, but the posterior part retains its transverse width (Fig. 5B). The scapular component of the glenoid is circular in outline, slightly concave in all directions, and faces ventrally and somewhat posteriorly.

On both sides of the specimen, the coracoid and procoracoid have separated and shifted slightly relative to one another, so the precise form of the coracoid plate is not certain. The coracoid forms practically all of the ventral facet of the glenoid. It faces dorsally,

posteriorly, and laterally, and is oval in outline with a slightly convex surface both transversely and anteroposteriorly. Below the glenoid, the hind edge of the coracoid is relatively wide, and it passes posteriorly into the characteristic therapsid posterior process. The external face of the coracoid is smooth and flat, except for the area below the glenoid, which is slightly convex from front to back. The anterior edge of the right coracoid is damaged, and that of the left coracoid obscured by the surrounding bones.

Only the right precoracoid is exposed. It is probably slightly larger than the coracoid, although this difference is not as marked as in *Ericiolacerta* (Watson, 1931). The anterior and ventral edges are thin, and the lateral surface flat and featureless. A notch in the posterior edge represents the anterior margin of the coracoid foramen.

Clavicle and Interclavicle (Fig. 5C, D)—There is no evidence for the splint-like cleithrum described by Watson (1931) in *Ericiolacerta*.

The two clavicles are fully preserved. Each one has a broad, thin plate medially that underlies the interclavicle (Fig. 5C). The shaft arises from the anterolateral part of the plate, attenuates rapidly in width to a rod-like form, and extends dorso-laterally. The distal end is slightly flattened in the transverse plane, where it lies against the anterior edge of the scapula (Fig. 5D). There is no specific acromion process developed on the scapula for its attachment.

The central part of the interclavicle (Fig. 5C) is obscured by the overlying clavicles. The anteriormost region is visible as a relatively narrow plate with a prominent mid-ventral keel. It does not appear to possess well developed lateral processes, although this is not certain. The posterior part of the interclavicle is exposed as a perfectly flat, very thin plate with no trace of a median ridge.

Sternum (Fig. 5C)—Rather unusually for therapsids, the sternum is fully preserved as a large, thin plate. The posterior part has an almost imperceptible median ridge, while a series of slight crenulations along the lateral and postero-lateral margins presumably indicate the points of attachment of ribs.

Humerus (Fig. 6A–F)—Both humeri are preserved, the right one still on the main block, and the left one removed along with the attached proximal ends of the radius and ulna. For descriptive purposes, a sprawling orientation of the forelimb is assumed, with the humerus extending laterally from the glenoid and the radius and ulna vertical.

As befits the small size of this animal, the humerus is relatively very slender, with only modestly developed processes, as compared to other therapsids. The articulating surface of the head must have carried a substantial cartilaginous cap in life. Seen end on (Fig. 6E), it is a curved strip of unfinished bone extending for the full width of the head and including the proximal end of the delto-pectoral crest. The head is very slightly convex from top to bottom edges, and approximately linear from front to back.
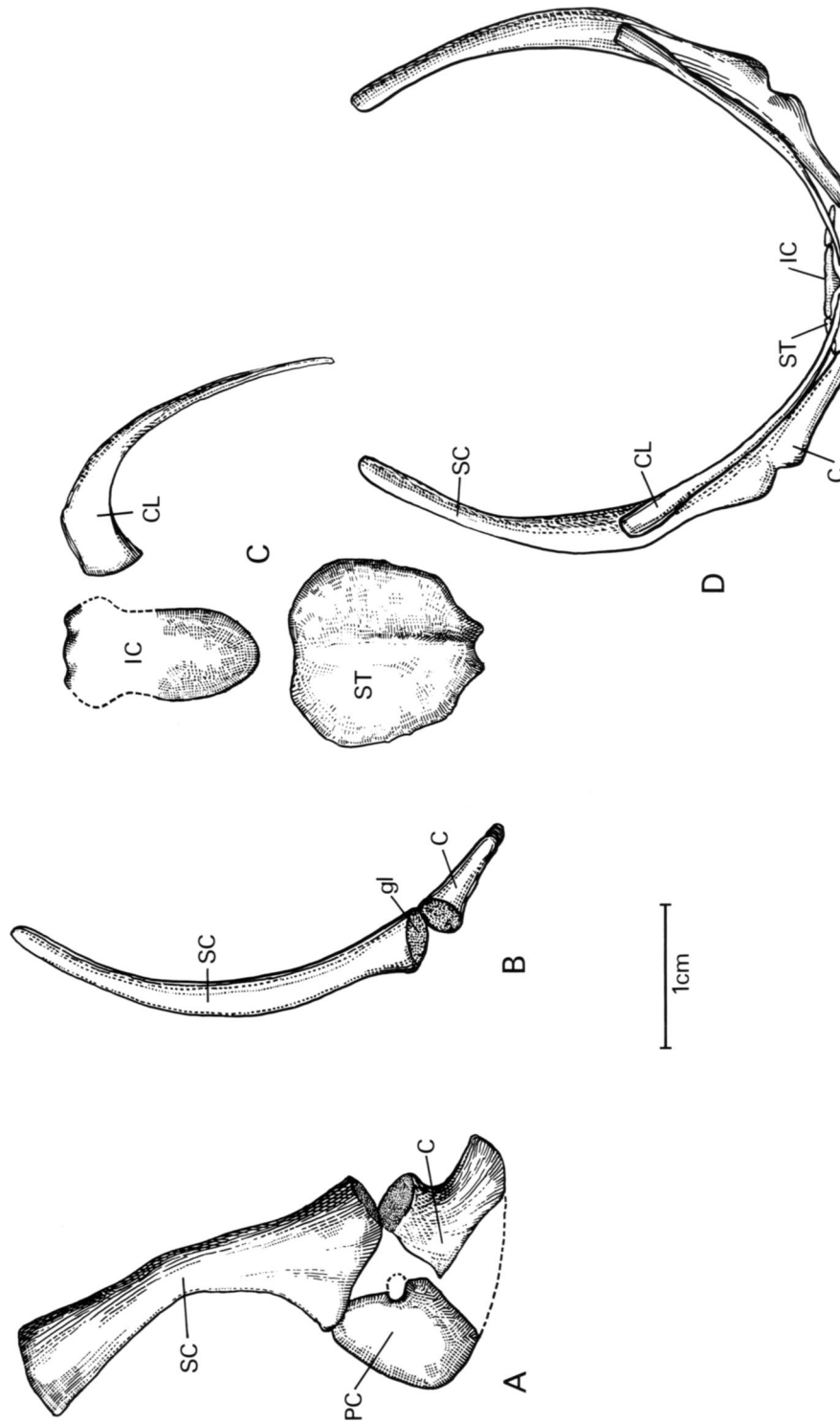
FIGURE 5. Regisauridae, indet. Pectoral girdle reconstruction drawn as left. **A**, lateral view of scapulo-coracoid; **B**, posterior view of scapulo-coracoid; **C**, ventral view of clavicle, interclavicle and sternum; **D**, anterior view of the whole pectoral girdle. Magnification ×2. Abbreviations: **C**, coracoid; **CL**, clavicle; **gl**, glenoid; **IC**, interclavicle; **PC**, procoracoid.
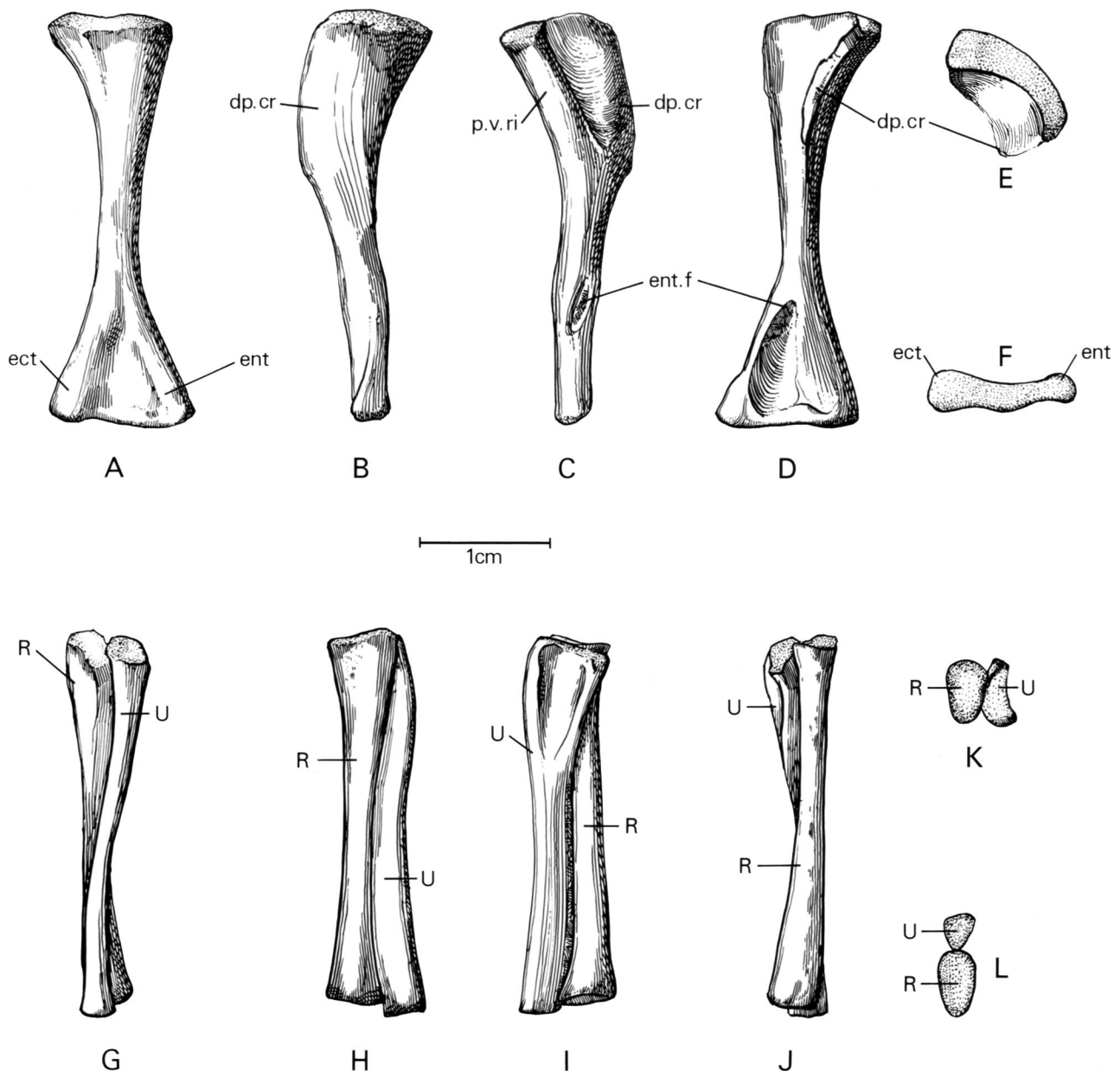
FIGURE 6. Regisauridae, indet. Forelimb bones drawn as left. **A**, humerus in dorsal view; **B**, humerus in anterior view; **C**, humerus in posterior view; **D**, humerus in ventral view; **E**, humerus in proximal view; **F**, humerus in distal view; **G**, radius and ulna in lateral view; **H**, radius and ulna in anterior view; **I**, radius and ulna in posterior view; **J**, radius and ulna in medial view; **K**, radius and ulna in proximal view; **L**, radius and ulna in distal view. Magnification ×2. Abbreviations: **dp.cr**, deltopectoral crest; **ect**, ectepicondyle; **ent**, entepicondyle; **ent.f**, entepicondyle foramen; **pv.ri**, postero-ventral ridge; **R**, radius; **U**, ulna.

In overall form the humerus is complexly curved. The planes of the expanded proximal and distal ends lie at about 35° to one another, while the proximal half of the bone curves dorsally relative to the distal half. The proximal half is broad, although much less so than in larger therapsids, and its dorsal surface is flat. The delto-pectoral crest arises smoothly from the anterior edge, and there is a definite, quite broad posterior face to the bone (Fig. 6C), well demarcated from the dorsal surface, and ending ventrally as a broad postero-ventral ridge. The ventral surface of the proximal half of the bone (Fig. 6D) is a broad, smooth trough limited anteriorly by the delto-pectoral crest and posteriorly by the postero-ventral ridge. The delto-pectoral crest itself is much less prominent than in larger therapsids, but has the same characteristic overall form.

The middle region of the humerus is approximately circular in cross section, beyond which the bone ex-

pands to form the wide distal region. There is no ect-epicondylar foramen, although a relatively large ent-epicondylar foramen in the posterior face (Fig. 6C) opens ventrally into a deep trough (Fig. 6D). The ect-epicondyle is not very expanded, and the entepicon-dyle only slightly more so. Between the two, the dorsal surface of the humerus is a smooth triangular trough (Fig. 6A). The ventral surface is fairly flat, apart from the groove of the entepicondyle foramen (Fig. 6D).

The articulating surface for the lower limb bones (Fig. 6F) faces distally, although it was undoubtedly completed in cartilage in life. It is strap-like in distal view, with expanded anterior and posterior parts and a very slightly expanded central part, all of which cor-responds to the shape of the transverse section of the distalmost region of the humerus.

Radius and Ulna (Fig. 6G–L)—The right radius and ulna are well preserved, in articulation with one another, and have been removed from the main block. The complete, but less well preserved bones of the left side remain on the block.

The radius has a pear-shaped proximal articulating surface, which is very slightly concave. The lateral crest of the bone is fairly prominent and ends proximally as a slight boss. The central part of the shaft is ap-proximately circular in cross section, and the distal part expands gradually in the lateral to medial direc-tion. The distal articulating surface is oval in form and again it is very slightly concave.

The ulna is almost exactly the same length as the radius, and it has a slightly sigmoid curvature. There is no ossified olecranon process and the proximal ar-ticulating facet is elongated in the lateral-medial di-

rection. The posterior face of the proximal part of the bone bears an extensive but shallow trough, limited laterally by a sharp ridge. The anterior part of the proximal region is not visible because it is overlain by the radius. Further down, the shaft is flattened antero-posteriorly in cross section, while the distal end ex-pands slightly anteriorly. The distal articulating facet is therefore semi-circular in outline, but considerably smaller than the distal end of the radius.

Manus (Fig. 7A)—Only a few isolated bones of the left manus are present on the main block. The right manus, however, is present and has been removed. It is incomplete and the bones are partly disarticulated, but it is adequate to indicate the size and some of the main features of the forefoot.

Two large bones lying at the proximal end are taken to be the ulnare and radiale, but the remaining set of carpals is incomplete and individually indeterminate. Metacarpals II to V are preserved parallel to one another and their respective lengths are determinable. A bone in the approximate position expected for metacarpal I is present, although it is comparable in both size and form to the rather scattered phalanges. However, it does resemble metacarpal I of the indeterminate bau-rioid figured by Watson (1931:text-fig. 27). The digits have been reconstructed somewhat imaginatively on the basis of the sizes of the few preserved phalanges.

THE PELVIS AND HINDLIMB

Parrington (1961) described briefly the pelvis and femur of this specimen in the course of his discussion of the origin of the mammalian femur. The pelvis is
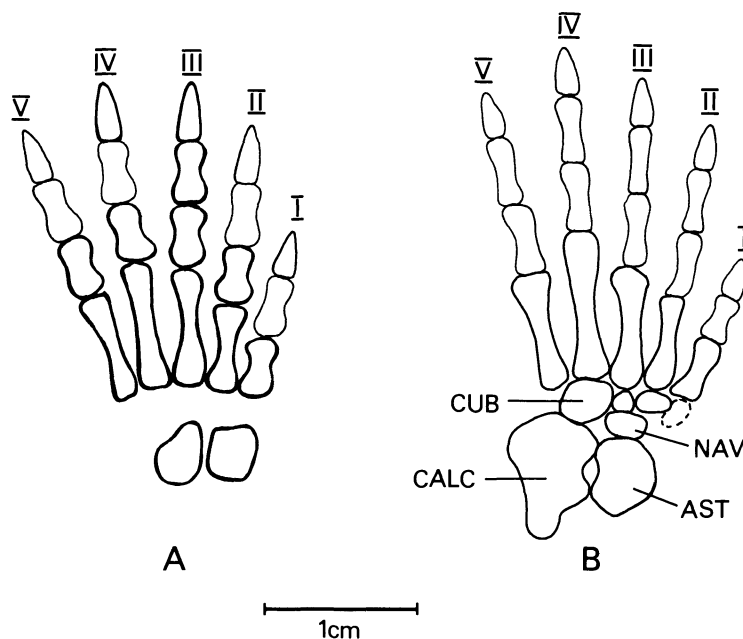

FIGURE 7. Regisauridae, indet. **A**, manus in dorsal view, identifiable bones heavy; **B**, pes in dorsal view. Magnification ×2. Abbreviations: **AST**, astragalus; **CALC**, calcaneum; **CUB**, cuboid; **NAV**, navicular.
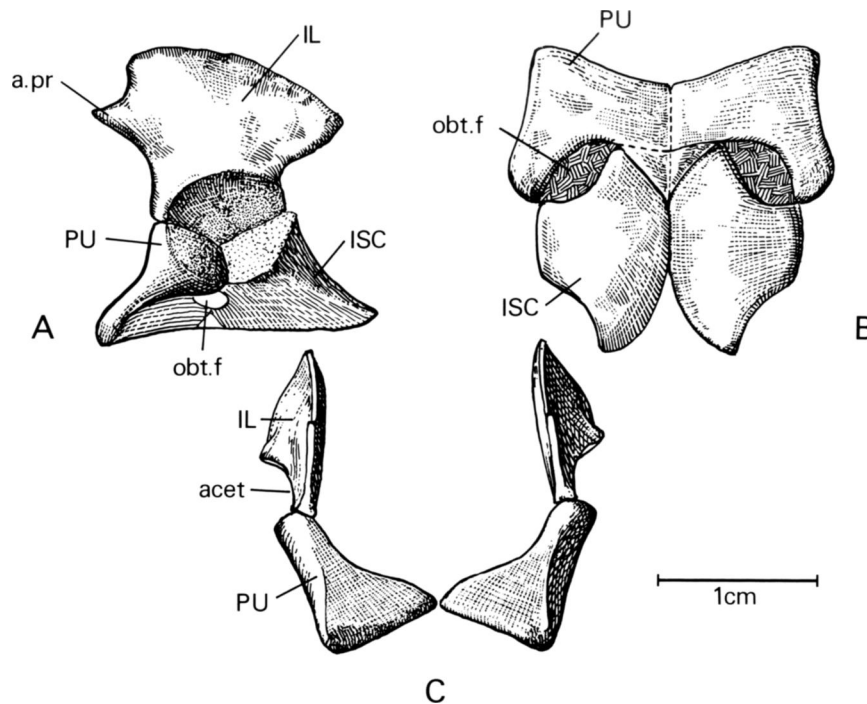
FIGURE 8. Regisauridae, indet. Pelvis reconstruction drawn as left. A, lateral view; B, ventral view; C, anterior view. Magnification ×2. Abbreviations: **acet**, acetabulum; **a.pr**, anterior process; **IL**, ilium; **ISC**, ischium; **obt.f**, obturator foramen; **PU**, pubis.

practically complete on both sides, although the right side is damaged. Unfortunately, the posterior part of the left ilium broke off and was lost, subsequent to the specimen having been figured.

The right femur, tibia, fibula and most of the pes are preserved and have been separated from the main block. The left femur and the proximal halves of the left tibia and fibula are also present.

Pelvis (Fig. 8)—The separate bones of the pelvis have shifted slightly relative to one another, and therefore their precise orientations are not certain. The ilia appear to diverge a little anteriorly, as confirmed by the relative lengths of the sacral ribs. The uniquely therocephalian feature of a delicate anterior process extending from the anterior edge of the ilium is well shown, as are the two broad depressions on the lateral surface (Fig. 8A). One lies between the anterior process and the dorsalmost point of the ilium, while the second occupies the posterior half of the bone. The supraacetabular boss lies immediately dorsal to the center of the acetabulum, but is not very prominent, perhaps in relation to the small size of the animal. The ilium forms almost half the area of the acetabulum and is deeply and evenly concave.

The pubis and ischium together form a large plate that is probably much closer to horizontally than vertically oriented, in contrast to other therapsids. The obturator fenestra between them is modest in size. The anterior edge of the pubis is thickened and extends antero-medially, while behind it the bone is a thin plate

that curves further medially. The pubic component of the acetabulum is oval in shape and has a slightly convex surface. The ischium is a large, thin plate oriented quite close to horizontal, as far as it can be reconstructed. The posterior region loses contact with its fellow in the mid-line, and flares laterally. The ischial part of the acetabulum is flat.

Femur(Fig. 9A–F)—For descriptive purposes, a sprawling orientation of the hindlimb is assumed, with the femur extending laterally from the acetabulum, and the crus aligned vertically.

Like the pelvis, the femur has a number of unmistakably therocephalian characteristics. It has a slightly sigmoid curvature, which has the effect of turning the head inwards towards the acetabulum. Also, the plane of the proximal end lies at an angle to the plane of the distal end, giving the bone the appearance of being twisted about its long axis (Fig. 9E). The proximal articulating surface is confined to the proximal end of the bone, and is convex both from front to back and dorsal to ventral. There are three trochanters distal to the head, the trochanter major along the posterior edge, the prominent internal trochanter mid-ventrally, and a small antero-dorsal trochanter, which is probably the functional equivalent of the mammalian trochanter minor (Kemp, 1978). A very slight ridge extends from the internal trochanter along the underside of the bone, all the way to the antero-ventral corner of the distal end of the femur. The distal end itself is only moderately expanded, and the entire distal end is occupied
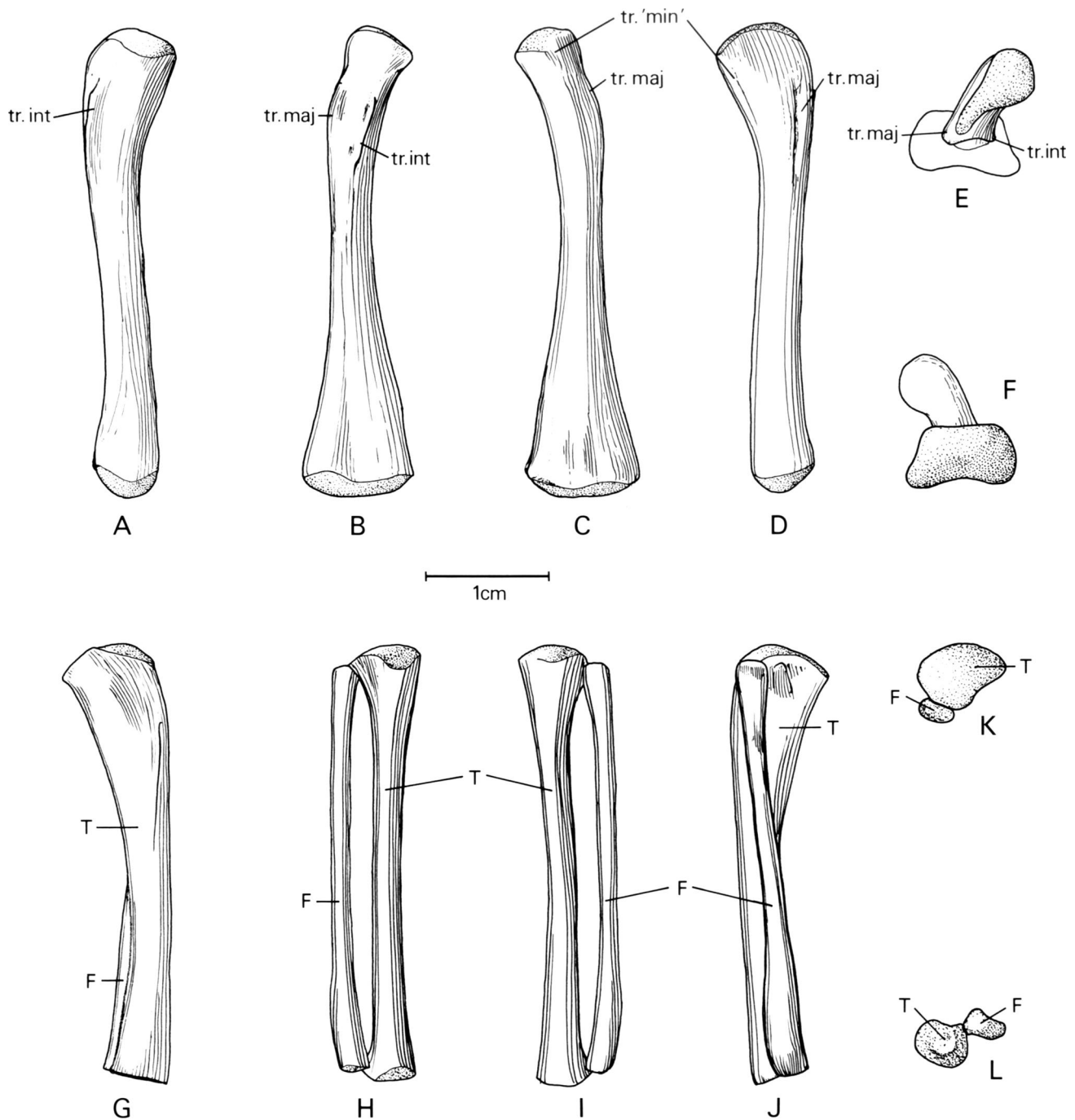
FIGURE 9. Regisauridae, indet. Hindlimb bones drawn as left. **A**, Femur in anterior view; **B**, femur in ventral view; **C**, femur in dorsal view; **D**, femur in posterior view; **E**, femur in proximal view; **F**, femur in distal view; **G**, tibia and fibula in anterior view; **H**, tibia and fibula in medial view; **I**, tibia and fibula in lateral view; **J**, tibia and fibula in posterior view; **K**, tibia and fibula in proximal view; **L**, tibia and fibula in distal view. Magnification ×2. Abbreviations: **F**, fibula; **T**, tibia; **tr.int**, trochanter internus; **tr.maj**; trochanter major; **tr.'min'**, trochanter 'minor'.

by the articulating surface for the tibia and fibula, although it must have been covered in cartilage in life.

Tibia and Fibula (Fig. 9G–L)—The right tibia and fibula are perfectly preserved and have been removed from the block in articulation with one another. Only the proximal halves of the left pair are present and have not been fully prepared.

The tibia and fibula are about 20% longer than the

radius and ulna, and the tibia is very slightly longer than the much more slender fibula. Both bones closely resemble those described in *Regisaurus* (Kemp, 1978).

The tibia is flattened antero-posteriorly. The lateral edge is almost straight compared to the strong concavity of the medial edge. The proximal part of the shaft therefore expands medially up to the articulating facet for the femur. The facet itself is gently convex in all directions. The distal part of the tibia is only slightly expanded, and terminates in a flat, approximately oval facet for articulation with the astragalus. The cnemial crest is represented by little more than a roughened surface on the lateral edge of the bone.

The fibula is almost straight, and very slender, with only a slight expansion of the shaft proximally and distally. The proximal articulating surface for the femur is a terminal oval; that for the calcaneum somewhat larger and flat.

Pes (Fig. 7B)—The right pes is preserved although the bones are slightly disarticulated, and many of the phalanges are missing. The edges of the tarsal bones are incompletely ossified.

The calcaneum and astragalus correspond closely to those of *Regisaurus* (Kemp, 1978). The calcaneum bears a prominent tuber calcis extending posteriorly and slightly ventrally from the roughly square main part of the bone. The lateral edge of the main body is raised as a definite dorsal ridge. The lateral and anterior edges of the calcaneum are very thin, but the medial edge is much thicker and bears an approximately vertical groove at mid-length. This corresponds to a similar groove in the lateral edge of the astragalus, and together the grooves form a canal that was interpreted in *Regisaurus* as the site of an astragalo-calcaneal ligament (Kemp, 1978). The astragalus itself is a more robust bone, with deep sides all around.

The cuboid, navicular, and second and third cuneiforms are present, but apart from their approximate sizes, little detail of the structure can be determined because of the incomplete ossification.

All five metatarsals are present. The fourth is substantially the largest, which is a slight difference from *Bauria* (Schaeffer, 1941), in which the fourth metatarsal is only slightly larger than the third and fifth metatarsals.

The phalanges are badly distorted, so the relative lengths of the digits shown in the reconstruction are rather tentative.

RECONSTRUCTION OF THE SKELETON

The near completeness of the specimen has allowed a reconstruction in which the sizes of the various bones have been drawn with confidence (Fig. 10). The relative orientations are, of course, rather more speculative. A slight dorso-ventral curvature of the vertebral column is suggested on no better criteria than the reduction of the ribs of the lumbar region, and the generally mammalian proportions of the skeleton as a whole. The shoulder girdle has been positioned so that the scapulo-coracoid matches the reconstructed shape of the ribcage while simultaneously positioning the glenoid to receive the head of a near-horizontal humerus. However, there can be little doubt that the shoulder girdle was mobile (see page 230), so the forelimb did not have a single, fixed orientation. The hindlimb has been given an alignment equivalent to that of a primitive, non-cursorial mammal (Jenkins, 1971b), with the knee turned well in but the femur still more or less horizontally oriented. A plantigrade stance is shown because of the lack of marked elongation of the metapodials that is associated with digitigrady in mammals.

The very mammal-like appearance of the skeleton is evidently due to the relatively long limbs, the attenuated lumbar ribs, and the greatly reduced tail.

JUVENILE CHARACTERISTICS OF "SCALOPOSAURS"

The specimen described in this paper would have been included in the Scaloposauria prior to Hopson and Barghusen's (in press) assertion that scaloposaurs are distinguished from other baurioid therocephalians only by juvenile characteristics. The characters that they mention are the small size, the broad intertemporal region, the incomplete postorbital bar, and the indistinct canine teeth. None of these can be taken as certain signs of immaturity. The size and the small canines could be adaptations to a particular way of life, while the intertemporal and postorbital features could be no more than allometric correlates of the small skull size. At present, no series of "scaloposaurs" that could be interpreted as a growth series has been described. Nor has a comprehensive study yet been done to relate particular "scaloposaurs" to particular mature therocephalian species.

The postcranial skeleton of the present specimen nevertheless offers support for the view that "scaloposaurs" are immature, in the form of the poor levels of ossification and the absence of tight sutures between bones. Both these features suggest that rapid growth was still occurring. Thus, the centra lack periosteal bone over the ends, and they are not fused to their respective neural arches. The odontoid is not synostosed to the axis centrum. In the lumbar and sacral regions, the ribs were sufficiently loosely attached to become disarticulated without damage. In both the pectoral and pelvic girdles, the bones have disarticulated slightly, again with no apparent damage. Finally, the carpals and the tarsals lack periosteal finishes around their edges.

COMMENTS ON THE FUNCTIONAL ANATOMY

The absence of epiphyseal ossification of the long bones, and the incomplete ossification of the articulating surfaces, make a detailed functional anatomical interpretation of the skeleton impossible. This is further compounded by the small size of the animal, and
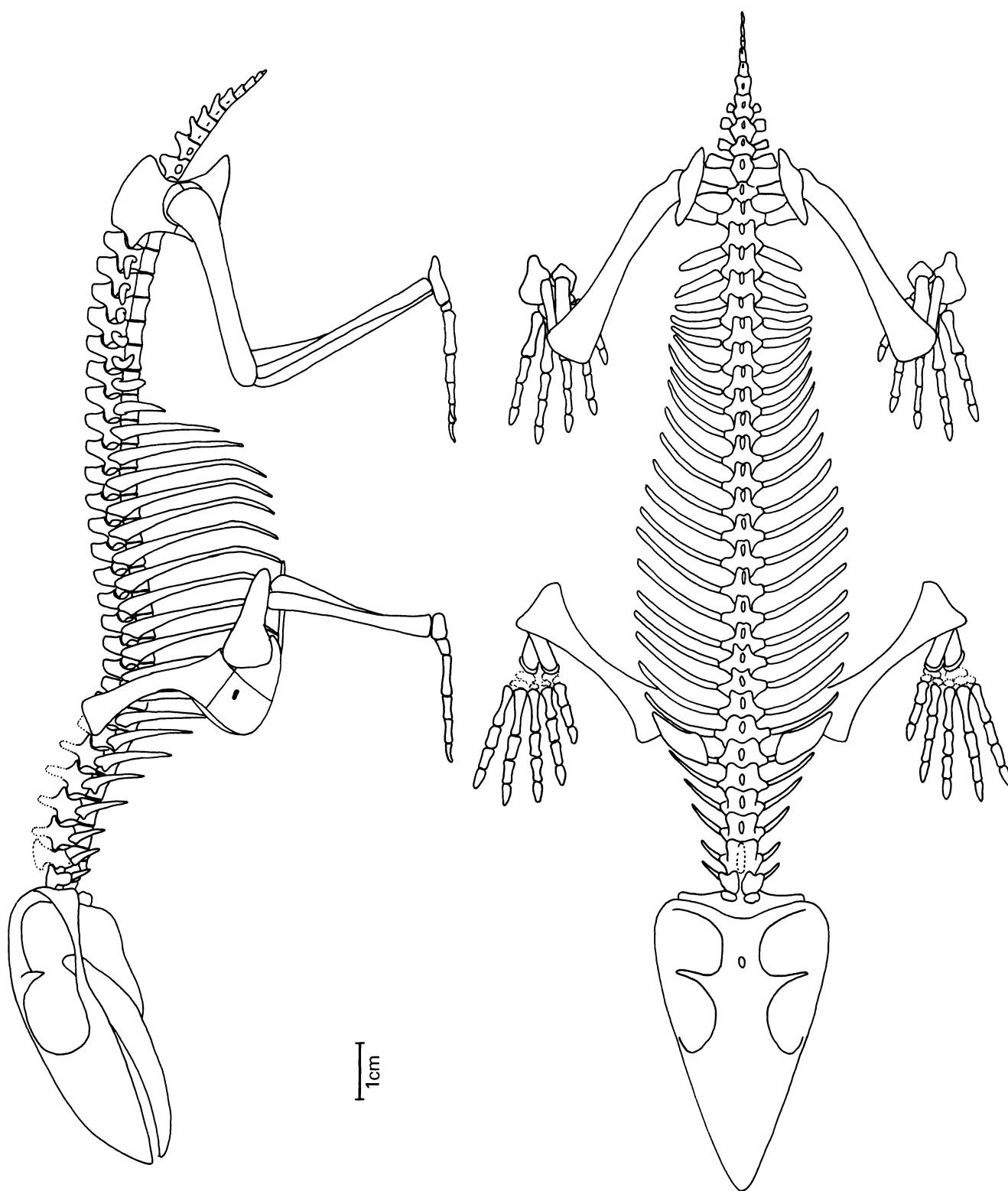
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FIGURE 10. Regisauridae, indet. Reconstruction of the complete skeleton. Natural size.

therefore the absence of clearly defined sites of muscle attachments. Nevertheless, a number of general observations may be made, particularly by comparison with the structure of other therapsids that have proved easier to study in this respect.

Atlas-axis Complex—The close similarity of these elements to those of cynodonts suggests that the movements were generally similar in both forms. The main difference is in the occipital condyle, which is partially obscured, but clearly resembles that described in *Regisaurus* (Mendrez, 1972). The condyle is effectively single and restricted entirely below the foramen magnum, although it is somewhat widened. Jenkins (1971a) pointed out that for extensive dorso-ventral movements of the skull on the atlas, a double condyle that has moved up alongside the foramen magnum is necessary, as in cynodonts. Therefore in this baurioid such movements were probably quite limited. On the other hand, the development of a cynodont-like atlas centrum, or odontoid, implies that rotational movements of the head plus atlas neural arches could occur, relative to the odontoid, as described in cynodonts (Kemp, 1969). A comparable system also occurs in dicynodonts (Kemp, 1969; King, 1981).

Differentiation of the Vertebral Column—The nature and degree of differentiation of cervical, thoracic, and lumbar regions of the vertebral column is also comparable to that of cynodonts, suggesting further functional similarities. The broad, near-horizontal zygapophyses of the cervical vertebrae indicate flexibility of the neck in the horizontal plane and also probably in the sagittal plane, but restriction of rotational movements about a longitudinal axis between adjacent vertebrae.

The articulating planes of the zygapophyses of the thoracic region are inclined to the horizontal, implying that lateral movements of this region of the column were reduced, a feature of all synapsids except certain primitive pelycosaurs such as *Varanosaurus* (Romer and Price, 1940; Kemp, 1982:61). The zygapophyses of the lumbar region have their articulating surfaces closer to horizontal than in such cynodonts as *Thrinaxodon* (Jenkins, 1971a), and are therefore more primitive. (In the primitive cynodont *Procynosuchus*, the zygapophyses are completely horizontal, but this is interpreted as a secondary specialisation for aquatic locomotion; Kemp, 1980a). In the present specimen, the implication is that a small degree of lateral undulation of the posterior part of the trunk still played some role in locomotion. The short, horizontally disposed ribs of the lumbar region are particularly reminiscent of cynodonts, including *Procynosuchus*. They may conceivably indicate the development of a transverse diaphragm, marking the posterior wall of the rather well-defined thoracic rib-cage, as has been suggested in cynodonts (Brink, 1956b; Kemp, 1980a). They may also correlate with mammal-like features of the organisation of the hindlimb and its musculature.

The three sacral vertebrae probably represent the primitive therapsid number.

The exact length of the tail has been established for very few therapsids. In the present case, the undoubted extreme reduction clearly shows that the pelvic musculature was modified from the primitive condition, the caudi-femoralis complex being replaced functionally by the ilio-femoralis, or gluteal complex (Kemp, 1978).

Forelimb—There are good reasons for believing that the shoulder girdle was mobile relative to the rib cage, and that this played a significant role in the locomotion of the animal (Kemp, 1982). Compared to pelycosaurs, which represent the primitive synapsid condition of the postcranial skeleton, the scapular blade is very narrow and has its contact with the clavicle reduced to little more than a point. The ventro-lateral edge of the coracoid plate may have contacted the interclavicle and sternum, as reconstructed by Watson (1931) in *Ericiolacerta*, but certainly there was no extensive overlap between these respective elements. Therefore the scapulo-coracoid was relatively free of bony constraints to movement. Furthermore, the clavicle is disposed almost horizontally between the interclavicle and the scapula, an arrangement analogous to that found in modern claviculate mammals, where extensive shoulder girdle mobility occurs (Jenkins, 1974).

The exact nature of shoulder girdle movement is more speculative. The broad expansion of the medial end of the clavicle, which underlies the interclavicle, indicates that the clavicle might have rotated in a horizontal plane about its medial end. The effect would have been a more or less antero-posterior shift of the scapulo-coracoid.

The scapular blade has not developed the lateral fossa characteristic of cynodonts. (This fossa is usually taken as evidence for the evolution of mammal-like spinatus musculature in cynodonts, e.g. by Jenkins, 1971a, but Kemp, 1980b, has challenged such an interpretation.) The relative size of the coracoid plate, and the form of the glenoid cavity, match those of primitive therapsids in general (Kemp, 1982), and therefore it is likely that the action of the forelimb was also primitive, characterized by a horizontally-oriented humerus moving in a sprawling fashion, as indicated in the reconstruction of the skeleton (Fig. 10).

Hindlimb—The anatomy of the pelvis and hindlimb closely resembles that of *Regisaurus*, which has been analysed functionally by Kemp (1978). The principal conclusion was that the hindlimb could operate facultatively in at least two different modes. One was a primitive, "sprawling" mode with the femur moving in a horizontal plane. The second was a mammal-like mode, with the femur extending almost forwards and moving in an approximately parasagittal plane. This interpretation explains many of the features of the bones, particularly the form of the hip joint, the orientation of the trochanters of the femur, the moveable

joint between the astragalus and the calcaneum, and the apparent positions of the major hip muscles. The actual specimen of *Regisaurus* available lacked the pubo-ischiadic plate and the pes distal to the astragalus and calcaneum.

The pubo-ischiadic plate is compatible with the dual-gait hypothesis. It has retained a fairly prominent anterior extension of the pubis, and therefore the pubo-ischio-femoralis internus musculature was probably well-developed. This would be expected to extend from the internal surface of the pubis and ischium forwards, around the anterior edge of the pubis, and backwards to the femur. In reptiles generally it functions as the major protractor muscle of the femur during a sprawling gait. On the other hand, the near-horizontal orientation of the pubo-ischiadic plate indicates that the femur was able to lie closely alongside the pelvis, while still possessing adductor musculature (pubo-ischio-femoralis externus) of adequate fiber-length. This is necessary if the limb is to be capable of acting in a parasagittal plane, in a mammalian fashion.

The reconstruction of the skeleton (Fig. 10) shows the hindlimb in its presumed parasagittal mode.

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