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Malerisaurus, A New Eosuchian Reptile from the Late Triassic of India

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MALERISAURUS, A NEW EOSUCHIAN REPTILE FROM THE LATE TRIASSIC OF INDIA

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[Plate 1]

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Two almost complete skeletons of a new eosuchian reptile, *Malerisaurus robinsonae* n.sp., were discovered as the presumable gastric contents of 'twin' skeletons of *Parasuchus hislopi*. The specimens are from fluvial flood plain deposits of the late Triassic Maleri Formation of the Gondwana supergroup, India.

The osteology of *Malerisaurus* is described in detail. *Malerisaurus* was a small, gracile, long-necked eosuchian, facultatively bipedal, and probably able to climb trees or to take to the water when alarmed. It is comparable to modern bipedal lizards in size, proportions and inferred activities. The skull, although showing some carnivorous adaptation, is relatively unspecialized and indicates an insectivorous diet.

Because *Malerisaurus* shows such a combination of primitive and advanced features as a diapsid skull, unossified laterosphenoid, lack of antorbital and mandibular fenestrae, slender limbs, primitive girdles, distinctive elongated cervicals and lack of dermal armour, it is assigned to the suborder Prolacertiformes of the order Eosuchia. A classification of Prolacertiformes indicates four families within this suborder: Petrolacosauridae, Protorosauridae, Prolacertidae and Tanystropheidae. *Malerisaurus* is tentatively allied to *Protorosaurus* in the family Protorosauridae; in neither genus is the temporal region of the skull adequately known. *Malerisaurus* furnishes detailed information about the skeletal morphology of what may be a hitherto undocumented lineage of eosuchian reptiles.

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1. INTRODUCTION

In the winter of 1965–6, two nearly complete and articulated parasuchian (phytosaur) skeletons were found in the late Triassic Maleri Formation of India. These skeletons show an uncommon association of prey and predator. Inside the rib cage of each parasuchian are the ingested bones of a small eosuchian reptile. A detailed description of the Maleri parasuchian, *Parasuchus hislopi*, is given elsewhere (Chatterjee 1978). In this present study, the ingested eosuchian material, *Malerisaurus robinsonae*, n.sp., is described.

This unusual preservation permits a more detailed analysis than is generally possible for small Triassic eosuchians. *Malerisaurus* shows most of the morphologic features of the suborder Prolacertiformes of the order Eosuchia (*sensu* Romer 1966). The Prolacertiformes are the long-necked eosuchians, small to medium-sized with gracile proportions. They are known from the late Pennsylvanian to late Triassic sediments of the U.S.A., Europe, South Africa, India and Israel.

The new material described below considerably amplifies our knowledge of the relationships of eosuchian genera, and of the phylogeny and classification of Prolacertiformes. This paper is a part of the series of studies on the Gondwana vertebrates by the Geological Studies Unit of the Indian Statistical Institute.

2. GEOLOGIC SETTING

The Gondwana sediments in India occur as strings of isolated basins, linearly arranged along several extant river valleys. They represent a fairly continuous sequence of terrestrial sedimentation from the Permian to the Cretaceous. In the Pranhita–Godavari Valley, the Maleri Formation is well known for its great variety of late Triassic vertebrates. It is a fluviatile, poorly sorted red-bed formation containing three lithologies: bright red silty clays; poorly sorted fine-grained white sandstones; and lime-pellet rocks (Robinson 1971). The clays are unlithified and normally form the flat low ground, whereas the sandstones and pellet rocks are cross-bedded and stand out as elongate mounds and ridges. The regional dip is about

TABLE 1. TRIASSIC SEQUENCES IN THE PRANHITA–GODAVARI VALLEY AND THE ASSOCIATED VERTEBRATE FAUNA

formation	main lithologies	characteristic fossils	age
Dharmaram	sandstone with red clays	plateosaur, thecodontosaur	late Upper Triassic (Upper Norian and Rhaetean)
Maleri	sandstones, red clays and lime-pellet rocks	dipnoi, metoposaur, rhynchosaur, parasuchian, aetosaur, traversodont, coelurosaur, thecodontosaur, eosuchian	early Upper Triassic (Carnian through Early Norian)
Bhimaram sandstone	sandstone with intercalated red clays	fragmentary remains, indeterminate	(? Ladinian)
Yerrapalli	red clays and sandstones	capitosaur, ?brachyopid, dicynodonts, erythrosuchid, trirachodont, rhynchosaur, eosuchian	middle Triassic (Anisian)

PLATE 1. Postcranial skeleton of *Malerisaurus robinsonae*, n.sp.; specimen ISIR 151; scale indicates 10 cm.

10–15° to the NNE and the sediments are undeformed but dissected by numerous faults. The estimated thickness of the Maleri Formation is 350 m in the type area.

All vertebrate localities occur within the clay facies, presumably a series of flood-plain deposits (Kutty 1969; Sengupta 1970). Sandstones and lime-pellet rocks are channel and interchannel deposits, and are usually poor in organic remains. A considerable fauna of rhynchosaurs, parasuchians, metoposaurs, traversodonts, aetosaurus, eosuchians and coelurosaurs has been collected recently from the Maleri Formation, and the Triassic sequence in the Pranhita–Godavari Valley is as shown in table 1.

3. Preservation and preparation

The bones were embedded in a soft clay matrix and were easily prepared mechanically, with pin vice and brush. The ribs of *Parasuchus* were carefully removed to recover the new eosuchian bones lying beneath them (figure 1). The cranial elements of the eosuchian were dissociated and jumbled, but the postcranium shows the natural association and coiling of the body. Apparently *Parasuchus* orientated its prey head-first, like modern crocodiles, during initial capture, and swallowed the body whole.

All the eosuchian material was removed from the predator's abdominal cavity so that it could be studied in detail. The left and right individuals of *Parasuchus*, as seen from the rear, were numbered as ISIR 42 and ISIR 43. The corresponding ingested eosuchians were numbered ISIR 151 and ISIR 150. Both the specimens are of the same size and proportions. A list of the material is given in table 2 and the main measurements in table 3.

Table 2. List of material

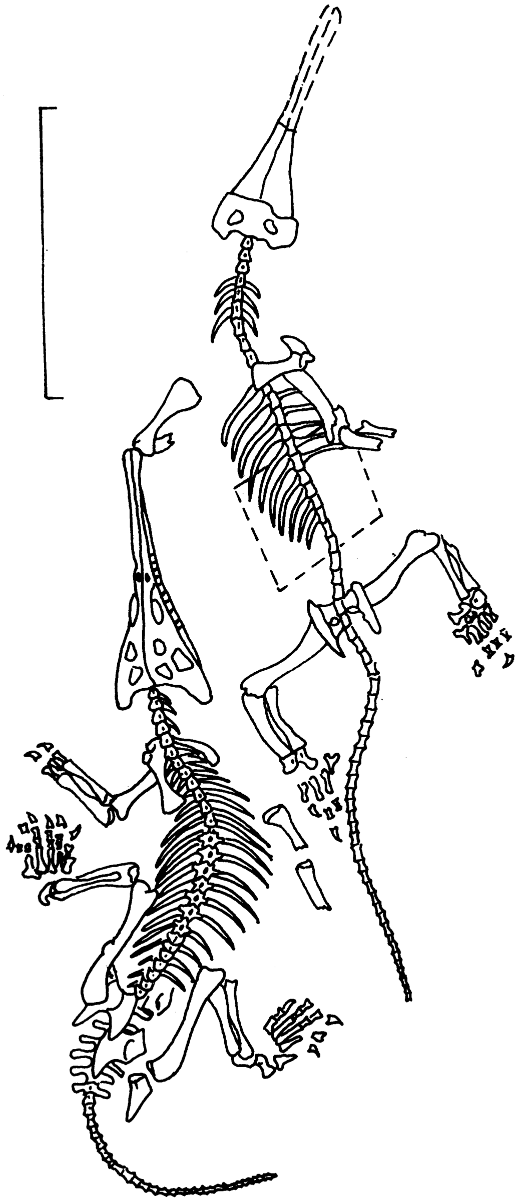
	specimen ISIR 150	specimen ISIR 151
skull	skull roof, palate, braincase, lower jaw; fragments shown in figure 2	only premaxilla and braincase; fragments 2, 19 in figure 2
vertebral column	6 cervicals, 16 dorsals, 2 sacrals and 5 caudals	9 cervicals, 10 dorsals, 2 sacrals and 13 caudals
shoulder girdle	scapula (r.)	scapulae (l., r.), coracoid (l.)
forelimb	humeri (l., r.), carpus and manus	humeri (l., r.), radius (r.)
pelvic girdle	ilia (l., r.), ischium (l.), pubis (l.)	ilia (l., r.), ischium (l.)
hindlimb	femur (r.), tibia (r.), phalanges	femora (l., r.), tibia (l.), tarsus and phalanges (l.)

Abbreviations: l., left; r., right.

The degree of ossification of the girdles, the vertebrae and the ends of the limbs suggests that the eosuchians, about 1.3 m long, were essentially mature when captured. By contrast, the parasuchians, although twice as long as their prey, were immature animals. Since the skull bones are better represented in ISIR 150, this specimen is designated as the holotype of *Malerisaurus*, and ISIR 151 as the paratype. All the material is housed in the Geology Museum, Indian Statistical Institute, Calcutta.

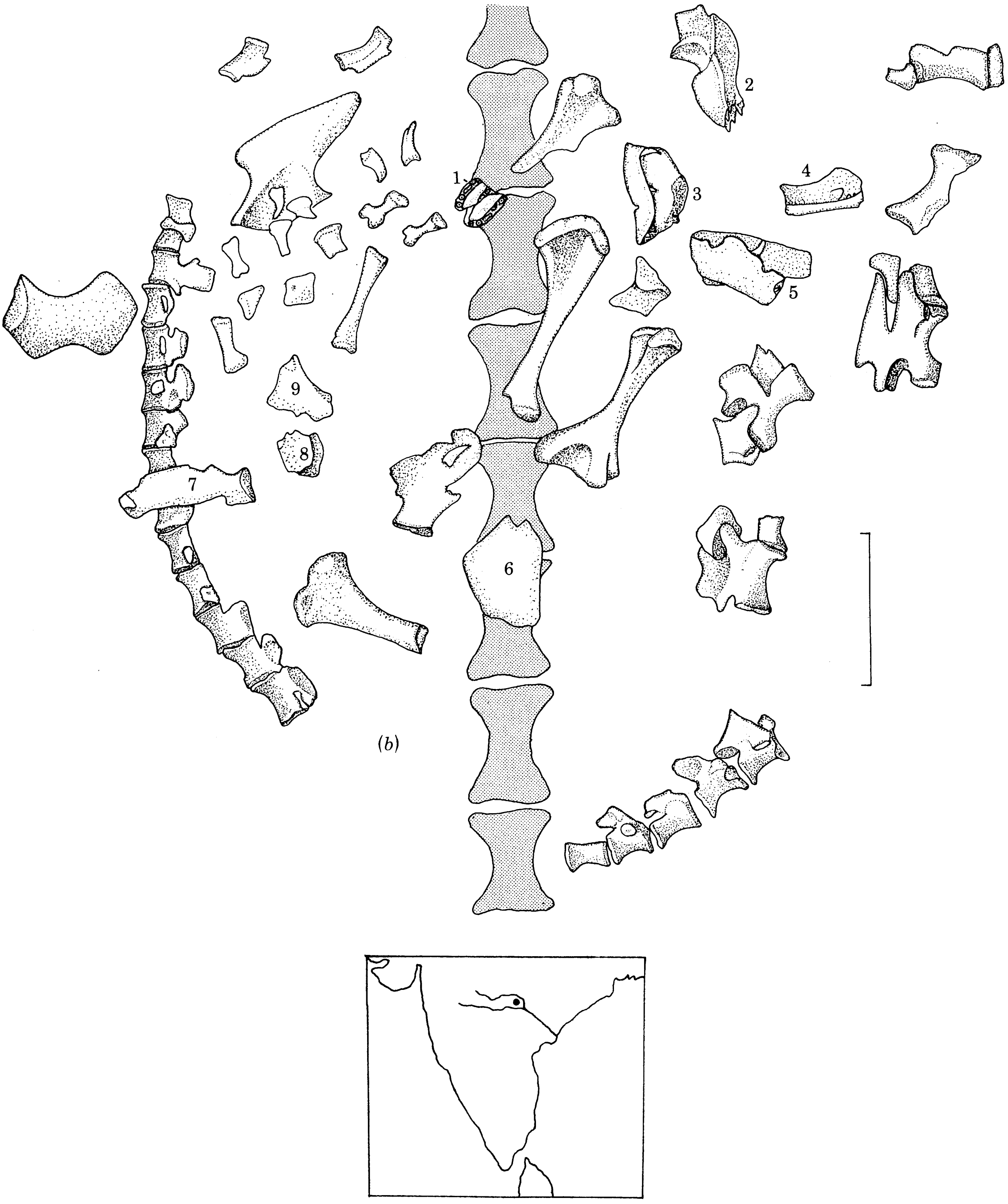
Table 3. Main measurements of *Malerisaurus robinsonae*
(Specimens ISIR 150 and ISIR 151. Measurements in millimetres.)

skull length	127
skull width	70
skull height	42
total length of the lower jaw	137
presacral column length	470
scapulo-coracoid height	53
breadth apex of the scapula	28
coracoid breadth	35
humerus length	63
humerus, least diameter of the shaft	7
radius length	55
radius, least diameter of the shaft	4
ilium, crest length	41
ilium height	39
ischium height	35
pubis height	26
total length of the pubo-ischiadic plate	67
femur length	100
femur, least diameter of the shaft	9
tibia length	100
tibia, least diameter of the shaft	6
pes length, including tarsus (estimated)	100
estimated total length	1300



(*a*)

Figure 1 *a*. For description see opposite.



(*b*)

(*c*)

FIGURE 1. (*a*) Two associated skeletons of *Parasuchus hislopi*, as found in the Maleri Formation of central India. Scale bar 60 cm. (*b*) The ingested bones of the eosuchian found in the right individual, as shown by dashed lines; specimen ISIR 150, holotype of *Malerisaurus robinsonae*, n.sp.; isolated eosuchian skull bones numbered 1–9; parasuchian vertebrae stippled. Scale bar 5 cm. (*c*) Locality map.

Notes on the reconstruction of Malerisaurus

The reconstructions are largely composites from both ISIR 150 and ISIR 151. The bones are illustrated as though they were all left elements. Most of the skull derives from ISIR 150, though part of the braincase and occiput are supplemented by ISIR 151. The quadrate in an upright position seems to be too tall with respect to the skull roof and so is reconstructed with slanting occiput. The missing bones of the skull are restored according to the pattern of other Prolacertiformes. The postcranial skeleton is better represented in ISIR 151 (plate 1).

4. Systematic palaeontology

class Reptilia
subclass Lepidosauria
order Eosuchia
suborder Prolacertiformes
family Protorosauridae
genus *Malerisaurus*, new genus

Type species. *Malerisaurus robinsonae*, new species.

Distribution. late Triassic Maleri Formation, India.

Diagnosis. Generic diagnosis same as for species, see p. 197.

Derivation of name. The generic name is based on the Maleri Formation from which the specimen was collected. The specific name honours the pioneer work in this region by Dr Pamela Robinson.

Malerisaurus robinsonae, new species

Holotype. ISIR 150: a nearly complete individual found between ribs and gastralia of articulated skeletons of *Parasuchus hislopi*; specimen ISIR 43.

Hypodigm. ISIR 151: another nearly complete individual except for the skull; found in same relationship to a second specimen of *Parasuchus hislopi*; specimen ISIR 42.

Type locality. Near Muttapuram village (lat.: 19° 8′ N; long.: 79° 40′ E), Adilabad District, Andhra Pradesh, India.

Horizon. Maleri Formation of the Gondwana supergroup in the Pranhita–Godavari Valley; late Triassic.

5. Osteology of *Malerisaurus*

Skull

The skull was clearly damaged during ingestion, making identification of individual bones difficult. Because of the incomplete nature of the material the skull osteology is somewhat interpretative. Nevertheless, the fragments do reveal many of the salient features. In the following discussion, the numbers in parentheses (1–19) refer to the bones as shown in figure 2.

The skull is long and narrow, monimostylic, and diapsid with a complete lower temporal bar. Snout elongation is clearly shown by the length of the maxillae, nasals and frontals. The dermal bones of the skull roof are smooth. The estimated skull length measured to the quadrate is 12 cm. The occiput is inclined, and the jaw articulation is behind the occipital condyle.

Skull roof (figures 3, 4)

The *premaxillae* (1, 2) are comparatively small, and extend backward and upward around the margin of the external nares to exclude the maxillae from these openings. The external nares are oval, subterminal and dorsally placed. The alveolar margin is straight and supports six small conical teeth in each side.

The *maxillae* (1, 3) form the main part of the snout; each is triangular in side view and carries about 13 teeth. The *nasals* (1, 4) are relatively narrow, elongate bones, which taper forward and show a thick medial edge. Posteriorly each bone has a shelf for the reception of the frontal. Part of the *frontal* (5) is preserved. It has a straight and thick mesial facet for articulation with the opposite frontal and a smooth and curved anterior rim for the orbit.

A thick unpaired symmetrical bone with finished posterior edge is identified as the *parietal* (6). The bone becomes deep anteriorly to house a ventral excavation presumably for the reception of the supraoccipital crest. The crista cranii are highly developed and form medial walls of the supratemporal fenestrae; each crista is pierced by a narrow canal. The lateral process of the parietal is broken off.

A conjoined and complex-shaped bone with smooth curved margin is thought to be a *prefrontal–lachrymal* bar (7), bordering the orbit. The prefrontal forms a triangular area on the skull roof and sends a ventral process reinforcing the lachrymal. Near the junction a foramen, possibly for the lachrymal duct, is present.

Another conjoined bone showing smooth rims on either side is recognized as the *jugal–postorbital* bar (8) between the orbit and infratemporal fenestra. The broad base of the jugal is missing. The posterior tip of the *squamosal* (9) is found in association with the left paroccipital process, receiving the latter in a ventral notch.

The partly preserved *quadratojugal* (19) curves posteriorly to make a broad contact with the quadrate. This contact clearly indicates that, unlike in prolacertilians, the quadratojugal is not atrophied, and the lower temporal arcade is probably complete.

The *quadrate* (10) is tall and narrow and slants backward. Its mesial edge, though broken, shows the usual shelf for the reception of the pterygoid. Laterally a large quadrate foramen, shared by the quadratojugal, is present below the midheight. The junction between the quadrate and the quadratojugal seems to be strong and without any possible movement, and the ascending process of the quadrate terminates as a narrow flange under the squamosal without any broad cephalic condyle, indicating a non-streptostylic structure. The ventral articular surface is thick and compact, with distinct inner and outer condyles.

Palate (figure 4)

The *vomers* (11) are small elements with tapering anterior processes occupying the position between the palatal processes of the premaxillae and the palatines. Laterally they are notched by the choanae.

The *palatines* (12) are extremely long, sheet-like bones with a narrow median cavity. Each bone has a lateral trough into which two large and compressed teeth are implanted. The posterior border defines the anterior limit of the large palatine fenestra. Dorsally it has an ascending process sutured to the prefrontal pillar.

The palatal ramus of the *pterygoid* (12) is preserved. It extends forward as a tapering process and is separated from its counterpart by a narrow interpterygoid vacuity. Posteriorly each pterygoid ramus is crowded with numerous sharp and pyramidal teeth.

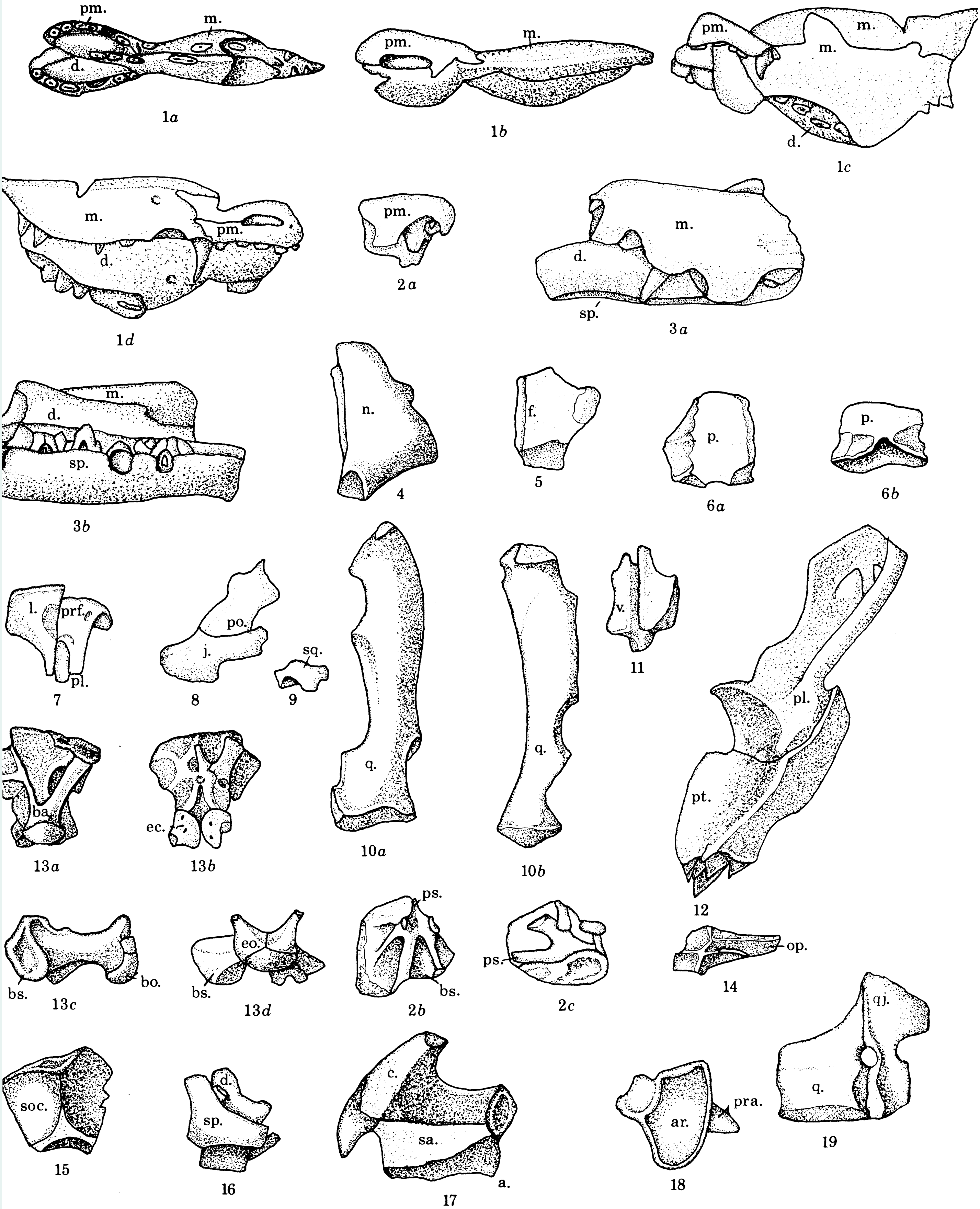


Figure 2. For description see opposite.

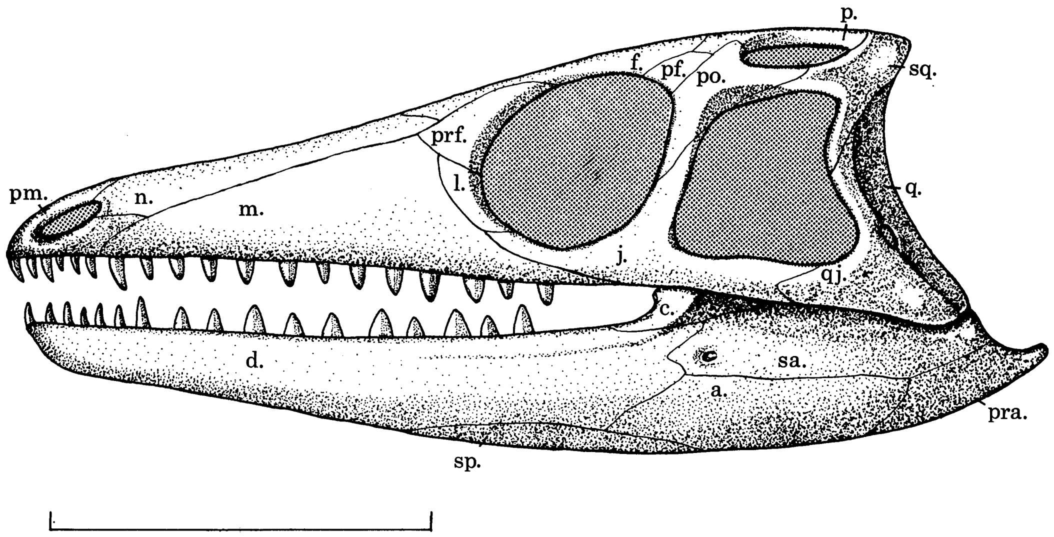


FIGURE 3. *Malerisaurus robinsonae*, n.sp. Composite restoration of the skull in lateral view. Scale bar 5 cm. For abbreviations, see legend of figure 2.

Braincase (figure 5)

The braincase structure, of primitive lepidosaurian grade without any ossified laterosphenoid, can be assembled from four preserved fragments (2, 13, 14, 15).

The *basioccipital* (13) is narrow and thick, with bifurcate basal tubera, and is fused to the basisphenoid. Dorsally it is sheathed by exoccipitals. The occipital condyle, formed mainly by the basioccipital, is hemispherical and comparatively small.

The *basisphenoid–parasphenoid* complex shows a parabolic depression on the ventral surface behind the basipterygoidal process (2, 13). At the roots of the processes paired foramina for the internal carotid arteries are visible. A little above the carotid canal lies the outlet for the facial nerve, near to the prootic suture. The cultriform process is slender, curves slightly upward, and extends forward in the interpterygoid vacuity. A shallow sella turcica lies dorsal to the base of the cultriform process.

FIGURE 2. *Malerisaurus robinsonae*, n.sp. Isolated skull fragments, numbered 1–19; all fragments except 2 and 19 belong to ISIR 150. Scale bar 5 cm. (1) Conjoined premaxillae, maxillae and dentaries; *a*, *b*, *c*, *d*, ventral dorsal, left lateral and right lateral views respectively. (2) Conjoined premaxilla and braincase; *a*, premaxilla, right lateral; *b*, basisphenoid, ventral view; *c*, parasphenoid-prootic, right mesial view. (3) Conjoined maxilla and lower jaw; *a*, left lateral view; *b*, left mesial view. (4) Left nasal, dorsal view. (5) Right frontal, dorsal view. (6) Parietal; *a*, dorsal view; *b*, occipital view. (7) Conjoined lacrimal, prefrontal and palatine, left lateral view. (8) Conjoined postorbital and jugal, left lateral view. (9) Left squamosal, anterior view. (10) Left quadratojugal: *a*, posterior; *b*, lateral view. (11) Vomers, palatal view. (12) Right palatine and pterygoid, palatal view. (13) Braincase: *a*, *b*, *c*, *d*, ventral, dorsal, left lateral and occipital views respectively. (14) Left opisthotic, anterior view. (15) Supraoccipital, postero-dorsal view. (16) Right dentary and splenial, mesial view. (17) Left coronoid and surangular, lateral view. (18) Right prearticular-articular, dorsal view. (19) Right quadrate and quadratojugal, posterior view.

Abbreviations used in this and later figures: a., angular; ar., articular; bo., basioccipital; bs., basisphenoid; c., coronoid; d., dentary; ec., ectopterygoid; eo., exoccipital; f., fenestra ovalis; i.c., internal carotid foramen; j., jugal; j.f., jugular foramen; l., lachrymal; m., maxilla; n., nasal; op., opisthotic; p., parietal; pf., postfrontal; pl., palatine; pm., premaxilla; po., postorbital; pr., prootic; pra., prearticular; prf., prefrontal; ps., parasphenoid; pt., pterygoid; q., quadrate; qj., quadratojugal; sa., surangular; soc., supraoccipital; sp., splenial; sq., squamosal; v., vomer; foramina for cranial nerves in roman numerals (V–XII).

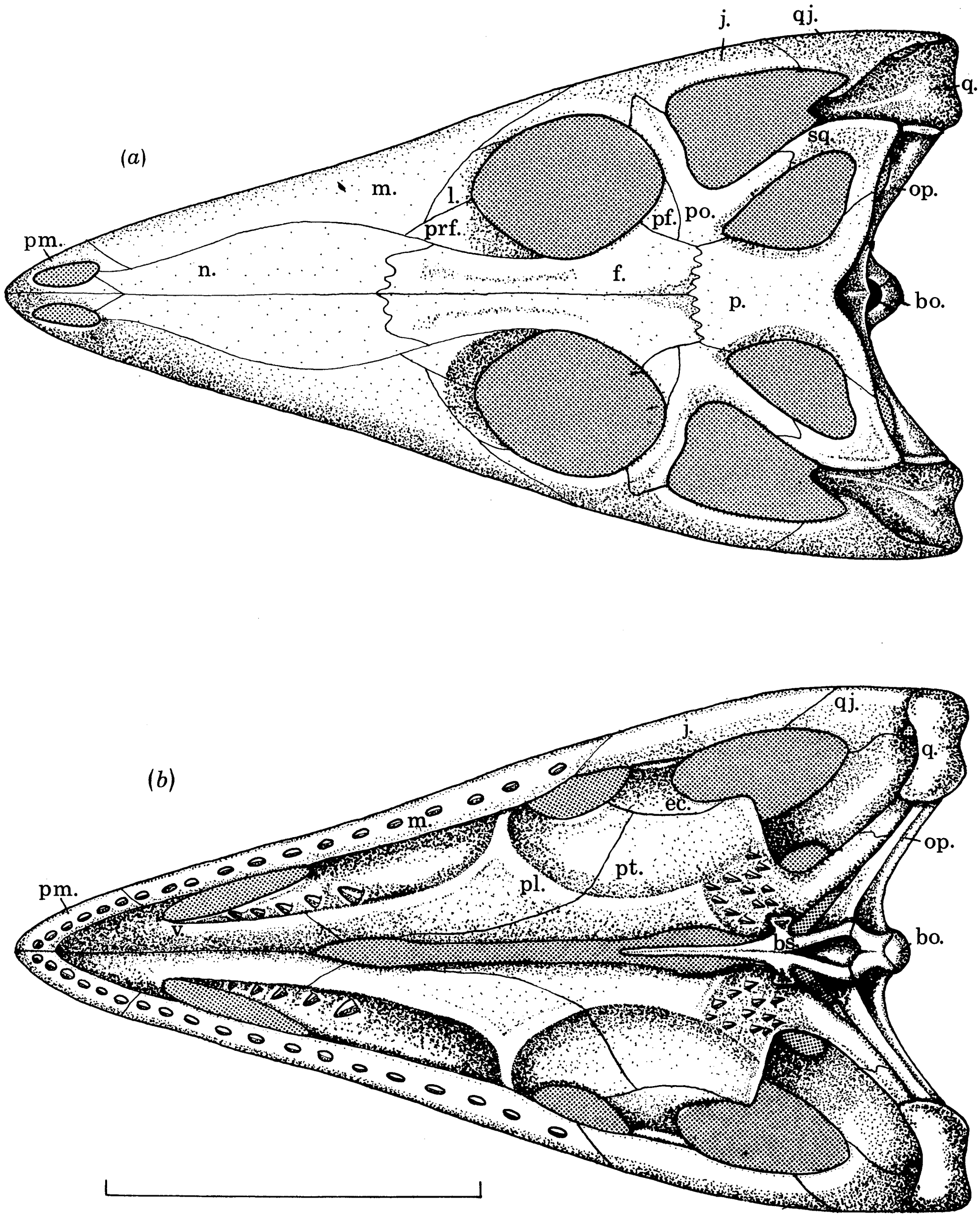


FIGURE 4. *Malerisaurus robinsonae*, n.sp. Composite restoration of the skull: (*a*) dorsal view; (*b*) ventral view. (Scale bar 5 cm.) For abbreviations see legend of figure 2.

Behind the sella turcica rises the highly developed dorsum sellae of the basisphenoid, pierced by a pair of foramina for the abducens nerve. Farther forward, the *prootic* (2, 13) has an open notch for the trigeminal nerve whereas posteriorly a tapering process extends from it to overlap the opisthotic.

The *opisthotic* (14) sends slender paroccipital processes laterally to abut the inner surface of the squamosal; this articulation is a loose one suggestive of kinesis. A large post-temporal fenestra is present above the paroccipital process. Antero-medially each opisthotic encloses a longitudinal stapedial groove leading into the fenestra ovalis. Part of the stapes is preserved in this stapedial groove. Below, a slit-like opening, separated from the fenestra ovalis by a thin bridge of bone, represents the jugular foramen, which transmitted nerves IX–XI and the posterior branch of the jugular vein.

The two *exoccipitals* (13) are sutured together over the basioccipital to form the floor of the hindbrain. They are confluent laterally with the opisthotics and each is pierced at the base by a pair of foramina for the hypoglossal nerve.

A symmetrical bone with a finished posterior edge is identified as the *supraoccipital* (15). The shape of the bone agrees well with that of a lepidosaurian except that it is a little thicker. It forms an arched roof over the foramen magnum. The anterior apex fits into the undersurface of the parietal, permitting some kinesis.

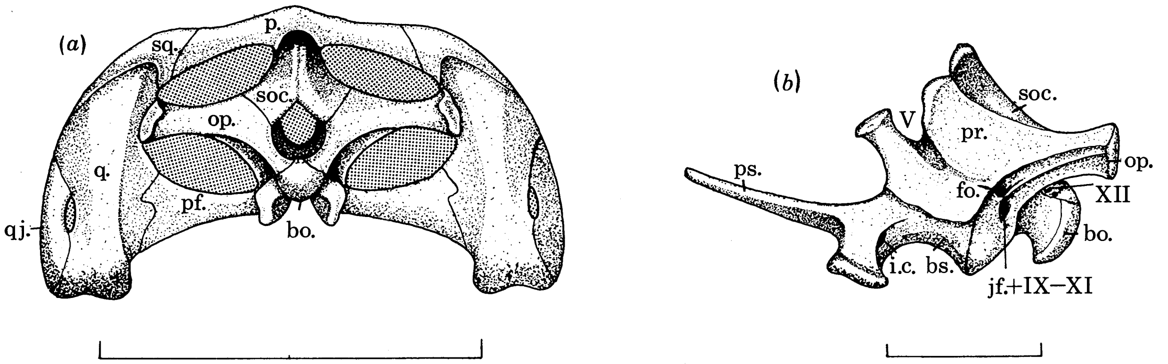


Figure 5. *Malerisaurus robinsonae*, n.sp. (*a*) Composite restoration of the skull in occipital view (scale bar 5 cm); (*b*) composite restoration of the braincase, lateral view (scale bar 1 cm). For abbreviations see legend of figure 2.

The lower jaw (figure 3)

The lower jaw is slender, compressed laterally, and shallow in the front but deeper to the rear. The jaw ramus is fairly straight and the symphysis seems to be loose and restricted to the dentary.

The *dentary* (1, 3) forms much of the lateral surface of the jaw. The anterior tip is pierced externally by numerous nutrient foramina. It bears about 17 teeth. The *splenial* (3, 16) comprises a considerable portion of the medial aspect of the mandibular ramus. Posteriorly it forks into two processes behind the alveolar border.

The *coronoid* (17) has an ascending process behind the dental margin and overlies the surangular. The *surangular* (17) is broadly developed on the outer surface, and extends back considerably where it is in contact with prearticular and articular. The *prearticular* (18) fuses with the articular posteriorly and forms a modest retroarticular process for insertion of the depressor mandibulae. With the quadrate in transverse position, the retroarticular process extends not only posteriorly but also mesially. Ventro-mesially it is pierced by the chorda tympani branch of the facialis nerve. The *articular* (18) supports a broad concave glenoid surface for the articulation with the quadrate condyle, indicating that the jaw movement was essentially orthal.

Dentition (figure 6)

(*a*) *Marginal teeth*

The dentition is imperfectly preserved. The marginal teeth are in a single linear series, borne on premaxilla and maxilla above and on the dentary below. They are cylindrical and show some degree of heterodonty. The anterior teeth are small and slim, closely spaced, recurved at their tips and circular or oval in section. The posterior teeth are large, straight and compressed laterally, with sharp edges front and back, and devoid of carinae. Since few teeth are intact, significant measurement of them is difficult. Measurements were made with an ocular micrometer fitted into a binocular microscope. In a fully erupted premaxillary tooth, crown height is 4.5 mm and crown width (antero-posterior) 2 mm; in a posterior maxillary tooth, the respective measurements are 4.4 mm and 3.6 mm. In the posterior dentary teeth, the crown height is 3.6 mm and crown width is 4.2 mm. It appears that the slenderness ratio (crown height/crown width) of anterior premaxillary tooth is higher than that of the posterior maxillary or dentary tooth.

The estimated dental formula is: premaxillary teeth, 6; maxillary teeth, 13; and dentary teeth, 17. The teeth have moderate cylindrical roots and are set in deep sockets to which they are attached by calcified connective tissue. The implantation is protothecodont (= subthecodont). Replacement activity is clear; empty alveoli and newly erupted teeth are encountered. At the lingual side of the jaw, various resorption pits can be seen at the base of the old teeth, through which small replacement teeth are visible. It appears that each replacement tooth migrated through the pits at an early stage to the pulp cavity of its predecessor and was thus in a position to replace it vertically when resorption of the old base was completed. Because of the incomplete nature of the material, the replacement pattern cannot be determined with certainty.

The posterior teeth show deep wear facets on the occlusal surface, along with signs of replacement activity. This indicates that either the tooth renewal was slow, as could be expected in the old stage of the animal, or food was hard and resistant.

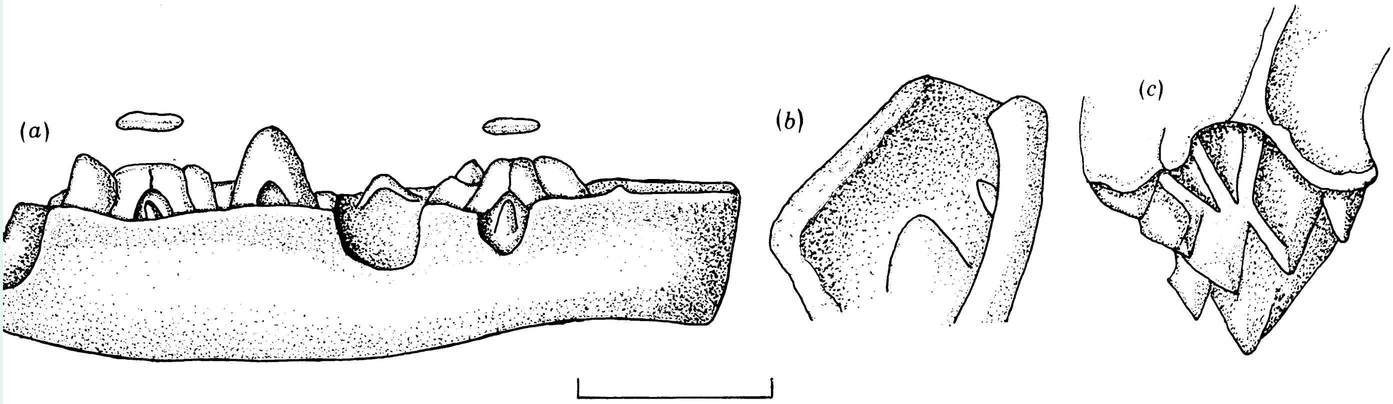


Figure 6. *Malerisaurus robinsonae*, n.sp. Dentition: (*a*) lingual view of the right dentary, showing replacement activity and tooth wear on occlusal surface; (*b*) palatal teeth; (*c*) pterygoidal teeth. Scale bar 1 cm.

(*b*) *Palatal teeth*

Teeth occur on the palatine and pterygoid. Two compressed and large teeth are found on the palatine. Pterygoidal teeth are numerous, small, sharply pointed and pyramidal in shape. The tooth field lies a little anterior to the basipterygoid articulation. The palatal teeth do not appear to be socketed but are attached directly to the bony surface of the mouth roof.

The vertebral column (figures 7, 8)

The vertebral column is well represented in both specimens. There are 25 presacrals, 2 sacrals and a string of 13 proximal caudals plus several isolated more distal caudals. All centra

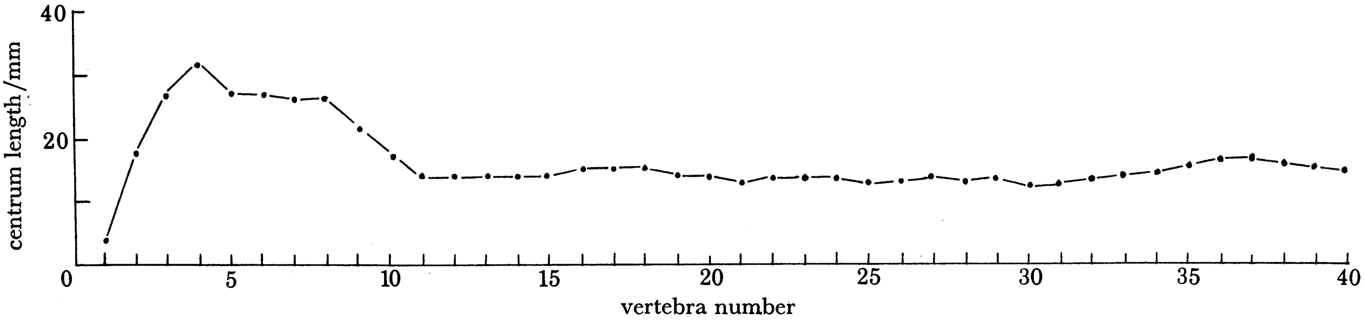


FIGURE 7. *Malerisaurus robinsonae*, n.sp. Chart of vertebral measurements, showing regional variation of centrum length.

are amphicoelous. No neurocentral sutures are visible. The vertebrae are regionally differentiated, showing marked variation in length between the cervicals (average centrum length 27 mm), which are roughly twice as long as the dorsals, the sacrals and the anterior caudals (average length 14 mm). There may be 9 cervicals and 16 dorsals, a common count in many lepidosaurs. No intercentra are present behind the atlas and the axis.

Presacral series

The vertebral column commences with a small proatlas bone, somewhat expanded anteriorly, which bridges the gap between the exoccipitals and the atlantal neural arch. The atlantal arch halves do not meet dorsally; they were presumably linked ventrally to the intercentrum by cartilage to form a ring-like structure. The convex odontoid has a notochordal pit at the centre A separate crescentic axis intercentrum is found below the odontoid. The axis centrum is shorter than the following cervicals and has a prominent midventral keel. Its neural spine is low but strong.

The seven following cervicals have elongate centra with distinct midventral keels and separate apophyses. The cervical centra are about three times as long as they are wide. The parapophysis is clearly developed and is situated low down on the anterior rim of the centrum. Just above it lies a narrow, weakly overhanging diapophysis far below the level of the neural canal, which is supported anteriorly and posteriorly by two lamellae. Of these, the latter is more extensive. Similarly low, appressed diapophyses are known in the elongate cervicals of *Prolacerta*, *Macrocnemus*, *Protorosaurus* and *Tanystropheus*. The zygapophyses are elongated anteroposteriorly well beyond the faces of their respective centra. The neural spines are very low and specialized. Dorsally each spine is as long as its respective centrum and although it touches its neighbours both front and back, it shows deep emargination anteriorly above the prezygapophyses, so that the postzygapophyses of the preceding vertebra can be inserted far back. This ensures more space to increase the mobility of the neck. The last cervical is transitional to the dorsal series; its centrum becomes shorter (length about twice diameter), the neural spine is somewhat narrower, the transverse process is more elongate and faces laterally and the parapophysis is higher on the centrum. The centrum retains its midventral keel.

In the first dorsal, the centrum is shorter still and lacks a ventral keel. The transverse process projects strongly laterally. The parapophyses are still on the centrum in the first four dorsals, but behind these they migrate onto the transverse processes. The dorsal, sacral and anterior

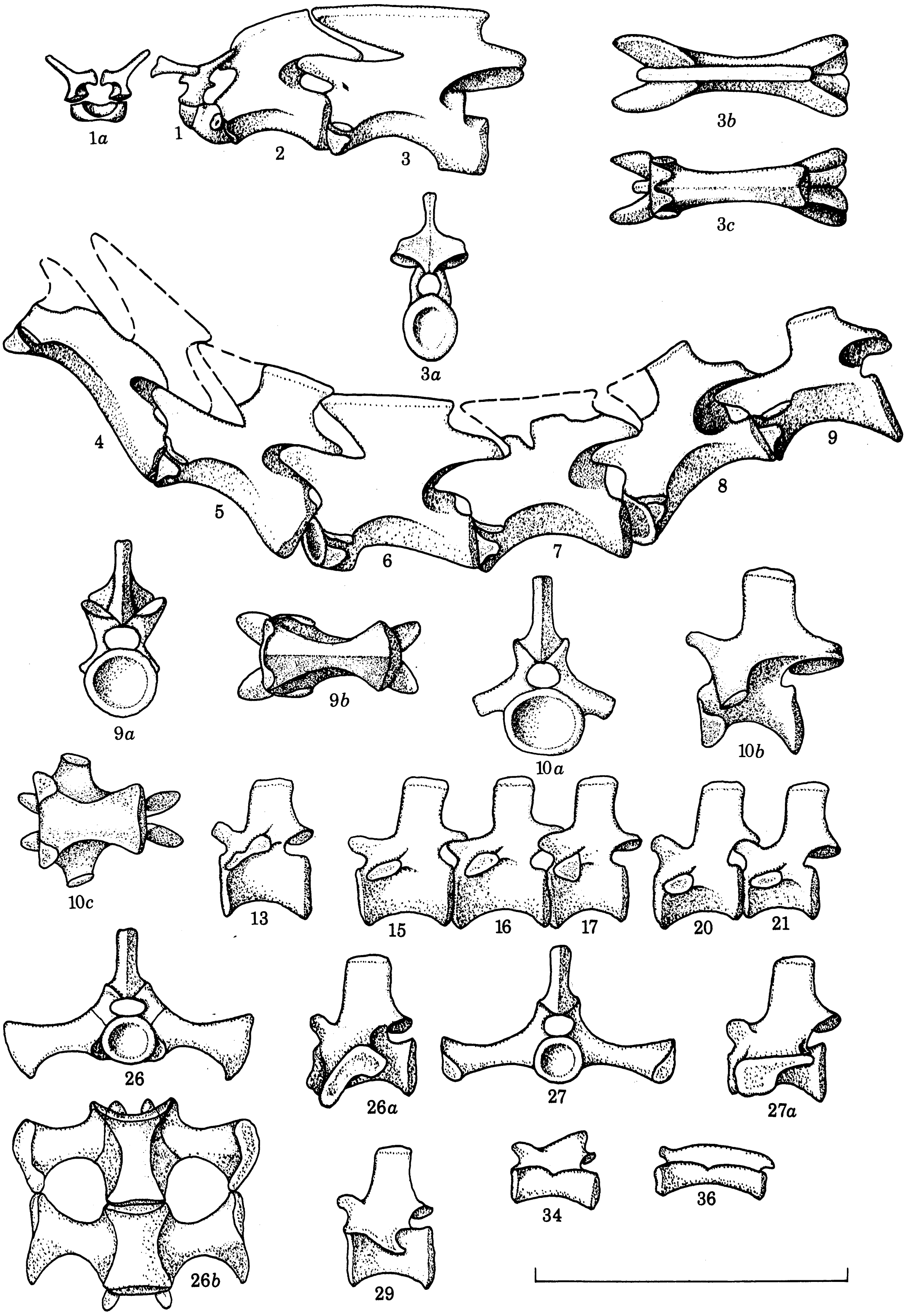


FIGURE 8. *Malerisaurus robinsonae*, n.sp. Vertebral column as numbered; composite restoration; 1–9, cervicals; 10–25, dorsals; 26 and 27, sacrals; 29–36, caudals. Scale bar 5 cm.

caudals are short, the centra having a length $1\frac{1}{2}$–$1\frac{1}{4}$ times the diameter of the centra. Vertebrae 13 and 14 bear elongated rib facets on the neural arches, where parapophyses and diapophyses are distinct and connected by a ventral ridge. From the 15th vertebra backwards, the rib articular facets gradually diminish in size and the two apophyses become confluent. In the dorsal series, the neural spines are taller and narrower than in the cervicals and the zygapophyses become smaller and more closely spaced posteriorly.

Sacrum

There are two unfused sacrals characterized by stout and distinctive ribs. In the first sacral, the ribs are sutured to the vertebra and each rib contributes a forwardly projected articular facet on either side of the centrum. In the second sacral the ribs are fused and lack accessory articular facets. The first sacral rib curves outward and backward while the second one curves outward and forward, the two ribs touching each other distally to afford a broad articular area for ilium. A large opening, the foramen sacrale, remains between the two ribs. The sacral centra have a build generally similar to that of the dorsals, but the zygapophyses are rather smaller.

Caudals

The first three caudals lack chevron facets and the vertebrae generally resemble those of the posterior dorsals except for the development of the pleurapophyses. From the fourth caudal backwards, the chevron facets are clearly seen on the posteroventral rim of each centrum, but no chevron bones have been found. Farther backwards, the centra become more slender and longer, the spines become very low and diminish gradually, the zygapophyses become very much smaller and closer to each other, and the pleurapophyses disappear. The tail must have been very long to counterbalance the long neck.

Shoulder girdle and forelimbs (figure 9)

The *scapula* is tall and narrow, with a thin waist and expanded ends. The antero-ventral edge shows a rugose acromial process for clavicular attachment. Except for the glenoid region, the scapular blade is thin, with an unfinished dorsal edge indicating cartilaginous extension of the suprascapula. The upper glenoid surface is semilunar and faces postero-ventrally. The coracoid portion of the glenoid is slightly concave, directed laterally and slightly posteriorly. The *coracoid* is considerably longer than it is wide and has a prominent postglenoid projection posteriorly. A coracoid foramen is present in front of the glenoid. The *clavicles* and *interclavicle* are not preserved in the collection.

The *humerus* is short with a slender shaft and appears to be primitive in that the proximal and distal ends are very wide, with a high degree of twist (about 70°) between them. The deltopectoral crest rises close to the head and bounds a large trochanteric fossa for insertion of the coracobrachialis brevis muscle. Distally the bone is divided into anterior and posterior condyles, the anterior the stouter, with distal articular surfaces for radius and ulna. On the anterodistal border is a deep ectepicondylar groove for the passage of the radial nerve and blood vessels.

The *radius* is slender with expanded ends and curved shaft. A concave, proximal facet receives the radial condyle of the humerus and permits rotary motion. The distal end is flat and oval in outline. The *ulna* is missing in the collection.

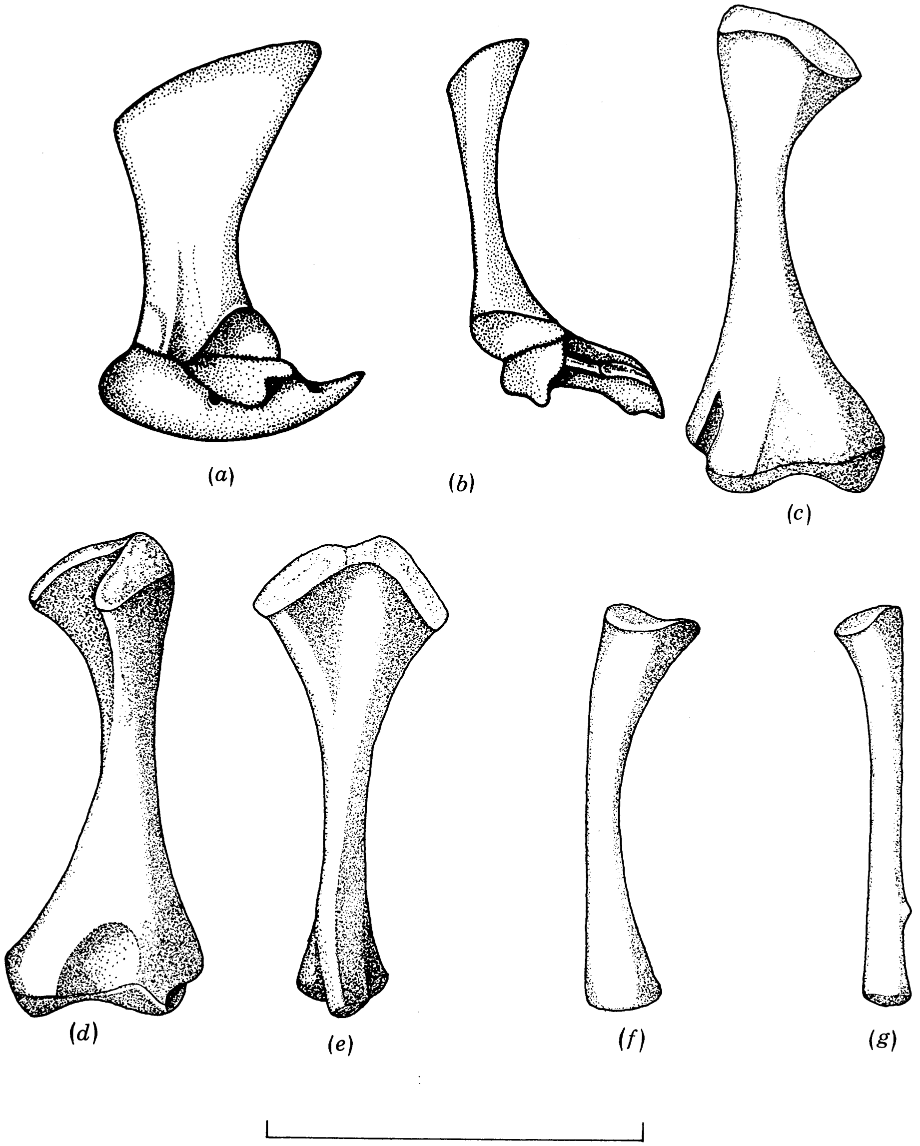


FIGURE 9. *Malerisaurus robinsonae*, n.sp. Shoulder girdle and forelimb. (*a*), (*b*) Lateral and posterior view of scapulocoracoid; (*c*), (*d*), (*e*) dorsal, ventral and anterior views of humerus; (*f*), (*g*) anterior and lateral views of radius. Scale bar 5 cm.

Two irregular squarish bones found in proximity of the radius are identified as *radiale* and *ulnare*. Other carpal bones, being isolated, are difficult to arrange in proper relationship. The claws are small, sharp and recurved.

Pelvic girdle and hindlimbs (figure 10)

The *ilium* has a strong posterior process tapering upward and backward and contains a deep depression externally for the caudofemoralis brevis. The anterior tip of the blade is short and thick and does not reach the anterior border of the ilium. The acetabulum is large, imperforate, and tear-drop in cross section, and has a prominent overhanging acetabular

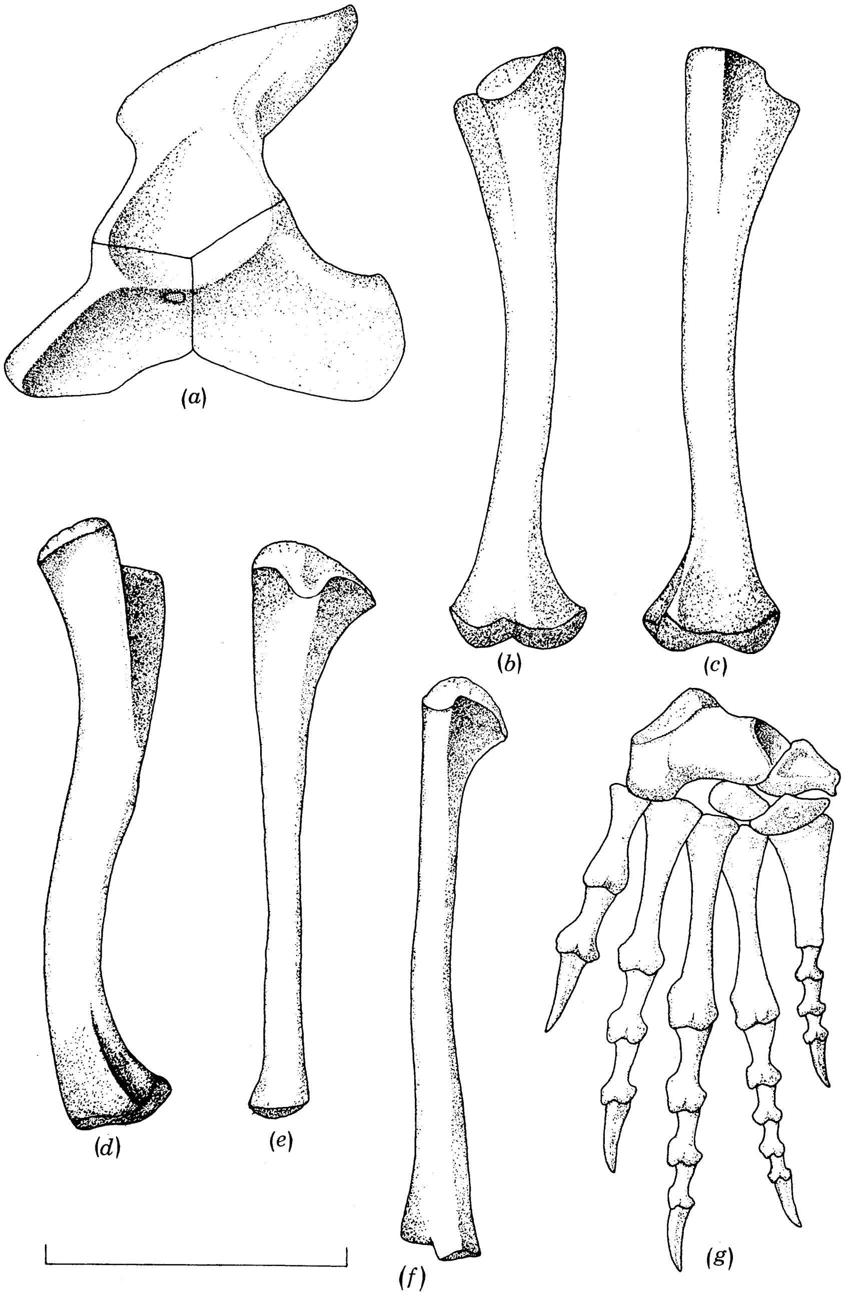


FIGURE 10. *Malerisaurus robinsonae*, n.sp. Pelvic girdle and hindlimb. (*a*) Composite restoration of the pelvis, lateral view; (*b*), (*c*), (*d*) dorsal, ventral and posterior views of femur; (*e*), (*f*) anterior and lateral views of tibia; (*g*) restoration of the pes, dorsal view. Scale bar 5 cm.

buttress. Above the acetabulum, the ilium is constricted to a neck, and above the neck the medial surface is excavated for the attachment of two sacral ribs.

The *pubis* and *ischium* are primitive, plate-like structures, dilated ventrally and curve gently toward the midline to form a deep and narrow V-shaped pelvic basin. The ossification along the symphysis is incomplete and a considerable notch is present ventrally between pubis and ischium, which was presumably filled by cartilage in life. The acetabular portion of the pubis is very thick and projects laterally, deepening the acetabulum anteriorly. Near the ischiadic contact a foramen for the obturator nerve is visible.

In specimen ISIR 151, the left femur is more slender and about 5 mm shorter than the right. I have observed similar asymmetry between right and left femora in two other Maleri reptiles, *Paradapedon* and *Parasuchus*, and it has been reported in *Typothorax* (Sawin 1947) and *Stagonolepis* (A. D. Walker, personal communication). Apparently the right hindlimb was more active in life than was the left hindlimb in those animals, this being a common feature in many vertebrates.

The *femur* is long and slender with a strong sigmoid flexure. The proximal articular head is hollowed, truncated and unfinished, presumably for a cartilaginous or epiphysial cap. The ventral surface of the head is occupied by a shallow intertrochanteric fossa with prominent internal trochanter. In the right femur of specimen ISIR 151, a small projection appears at midlength on the postero-ventral part of the shaft. The left femur of the same individual lacks this rugosity. This could be a pathological mark or an exostosis.

Distally the femur is broadened and divided into two condyles for tibial articulations. On the posterior aspect of the lateral condyle lies a longitudinal groove along which the fibula presumably slid.

The *tibia* has a broad triangular end, a very long and slender shaft, and slightly expanded distal ends. The proximal articular surface slopes down laterally towards the apex of the triangle and shows a weak cnemial crest anteriorly. Posterolaterally, a faint longitudinal groove behind the apex probably indicates the contact of the fibula. The distal expansion is at a large angle to the proximal one and shows a shallow ventral notch for the astragalus.

The *astragalus* is very large, almost twice as wide as the distal end of the tibia. The crural facets are well developed proximally, separated by a median notch. Distally it forms a convex rolling surface for the metatarsals I and II.

The *calcaneum* is highly reduced, and forms a combined facet with the astragalus for the reception of the fibula. It has a more or less well developed lateral process. Two *distal tarsals* are preserved, the lateral one is the larger and supports the unhooked fifth metatarsal. The ankle joint is mesotarsal, acting between proximal and distal tarsals.

The *metatarsals* and *phalanges* were found dissociated and somewhat damaged. The pes is restored in the fashion of primitive reptilian pattern with an assumed phalangeal count of 2–3–4–5–4. The claws are sharp, recurved, compressed laterally.

6. STANCE AND GAIT

Malerisaurus, as restored from the foregoing description, is a small, gracile reptile with a moderate-sized skull, followed by an elongate neck, relatively short trunk, and presumably a long tail. The limbs are slender and the hindlimbs are longer and more powerful than the forelimbs (table 4).

The backbone was evidently pliable with no sign of fusion or ossified tendons. In specimen ISIR 151, the articulated cervicals resemble an archer's bow. Here the anterior and posterior central surfaces form angles of 50–75° with the long axis of the centrum. Similar angling of postaxial centra occurs in various theropods (Ostrom 1969) and in modern fissipeds, most prominently in the lion and the tiger. This feature must be related to the natural upward curvature of the neck. Another conspicuous feature in the cervicals of *Malerisaurus* is the development of low, elongate neural spines, which are thickened at the summit and touch their neighbours. This suggests the presence of powerful nuchal ligaments, which supported the head and long neck without muscular effort in a high resting posture. In all long-necked animals this constitutes an antigravity mechanism (Hildebrand 1976). From this position a very small amount of energy is required to lower the head to the ground or raise it to full height. A small muscular tug depressed the head to the ground, simultaneously stretching the ligament. When the muscles relaxed, the ligament shortened and elevated the head. The outstretched zygapophyses in the cervicals allowed much flexibility in this region.

Table 4. Body proportions and indices of *Malerisaurus*

1.	$100 \times \dfrac{\text{skull width}}{\text{skull length}}$	55
2.	$100 \times \dfrac{\text{skull length}}{\text{length of presacral column}}$	27
3.	$100 \times \dfrac{\text{length of cervicals}}{\text{length of dorsals}}$	77
4.	$100 \times \dfrac{\text{length of (humerus + radius + manus)}}{\text{length of (skull + cervicals)}}$	37
5.	$100 \times \dfrac{\text{length of (humerus + radius)}}{\text{length of (femur + tibia)}}$	59
6.	$100 \times \dfrac{\text{length of (femur + tibia)}}{\text{trunk length}}$	74
7.	$100 \times \dfrac{\text{length of radius}}{\text{length of humerus}}$	63
8.	$100 \times \dfrac{\text{length of tibia}}{\text{length of femur}}$	100
9.	slenderness index $= 100 \times \dfrac{\text{least diameter of the shaft}}{\text{length of the limb}}$	
	(*a*) humerus	11
	(*b*) radius	7
	(*c*) femur	9
	(*d*) tibia	6

The limbs and girdles are good indicators of posture, and from this osteological evidence both Bakker (1971) and Charig (1972) recognized three grades of locomotion in archosaurs that are essentially walkers or runners: sprawling grade, semierect and fully erect. Almost all early Triassic thecodonts were sprawlers, where the humerus and femur were held almost horizontally and the body could be supported off the ground only with much work from the ventral shoulder and hip muscles. The semierect grade was exemplified by later pseudosuchians, aetosaurs, parasuchians and crocodilians. In these groups the femur is sigmoid with inturned head, the internal trochanter is lost, the fourth trochanter is developed and the tarsal joint is of a crocodiloid pattern. The fully erect grade was achieved by dinosaurs through various structural modifications: fenestration of the acetabulum to allow deeper penetration of the inturned head of the femur; straight limb shafts; increased number of sacral vertebrae for strong hip joints; strong iliac processes; and elongate and rod-like pubis and ischium.

None of these dinosaur hallmarks is present in *Malerisaurus*. On the contrary, many archaic features are encountered. The acetabulum is imperforate, the pubo-ischium is short and plate-like and the femur is sigmoidal with a terminal head and with a large internal trochanter. The latter limits the degree to which the femur could act in a vertical plane, and this degree is less than in many of the semierect thecodonts and crocodiles and in fully erect dinosaurs. *Malerisaurus* was probably tending towards semierect posture, and its sigmoidal femur might have allowed a certain degree of abduction.

The outstanding feature in the skeleton of *Malerisaurus* is its great limb disparity. In bipedal reptiles the hindlimbs are longer than the forelimbs, and the trunk region is relatively short. Thus both forelimb:hindlimb and trunk:hindlimb indices are useful in inferring the gaits of fossil reptiles.

It is not amiss here to compare various limb proportions of modern reptiles that are somewhat *Malerisaurus*-like in conformation. For this purpose I have used Ewer's (1965) data. Three groups of living reptiles were chosen: *Sphenodon* and *Varanus* as slow-running quadrupeds; *Agama* as a fast-running quadruped; and *Chlamydosaurus* and *Basiliscus* as facultative bipeds. In addition, *Euparkeria* is chosen as a fossil representative of a facultative biped.

Figure 11*a* shows the length of the forelimb as a percentage of that of the hind. With a forelimb length 59% of the hindlimb length, *Malerisaurus* is close to *Basiliscus*. This index is highly variable even among obligate biped theropods, as estimated by Ostrom (1969). It is 42% in *Allosaurus*, 45% in *Coelophysis*, 51% in *Ornithomimus*, 66% in *Ornitholestes*, 70% in *Deinonychus* and 26% in *Albertosaurus*. When the hindlimb and trunk are compared, *Malerisaurus* is in the same class as *Euparkeria* and is between the fast quadrupedal *Agama* and the facultatively bipedal *Chlamydosaurus*. From these comparisons it appears that *Malerisaurus* was very close to *Euparkeria* in general habitus and was facultatively bipedal. It was capable of running bipedally as effectively as could *Chlamydosaurus* and possibly as effectively as could *Basiliscus*.

Snyder (1949, 1952, 1962) observed that in resting position the hindlimbs of *Basiliscus* extend forward and laterally, with the shank flexed like that of a frog, whereas the forelimbs are only partially flexed. Both hands and feet point forward. When alarmed, *Basiliscus* is able to rise at once to the bipedal position by using the intrinsic extensor muscles without the forelimbs playing an important role in elevating the body. With the initial forward thrust of the hind limbs, the animal rises from the ground. Within a few strides it attains maximum speed, the femur is abducted and the pelvis yaws from side to side, rolling rhythmically about its longitudinal axis to avoid dislocation of the femur. In terms of economy of action this lacertian type of bipedalism is a primitive and inefficient method, the femur being held horizontally or obliquely, with its proximal end pulled inwards against the acetabular socket by components of force exerted by the extrinsic musculature. This arrangement necessitates a strong musculature to maintain the bipedal pose alone when the body is off the ground. By contrast, the femur of dinosaurs has a more vertical posture and its proximal end abuts the distal rim of the acetabulum without much muscular effort because of gravitational forces from the animal's own mass (Bakker 1971; Charig 1972).

A long tail plays an important role in reptilian bipedal locomotion because it acts as a counterpoise for the weight of the head and trunk and as a compensating mechanism for shifts in the centre of gravity. Snyder found, after amputation of the posterior two-thirds of the tail, that the bipedal posture of *Basiliscus* is no longer possible either when the animal is standing or when it is running. Although the tail of *Malerisaurus* is incomplete, it is very likely that the animal had a relatively very long tail.

The forelimbs of *Malerisaurus*, although relatively short, were probably used during slow locomotion. The glenoid is a saddle-shaped notch facing outward and backward, permitting humerus rotation, abduction and backswing. The close proximity of the deltopectoral crest to the head must have allowed the pectoral musculature good leverage for rotating the humerus about its long axis.

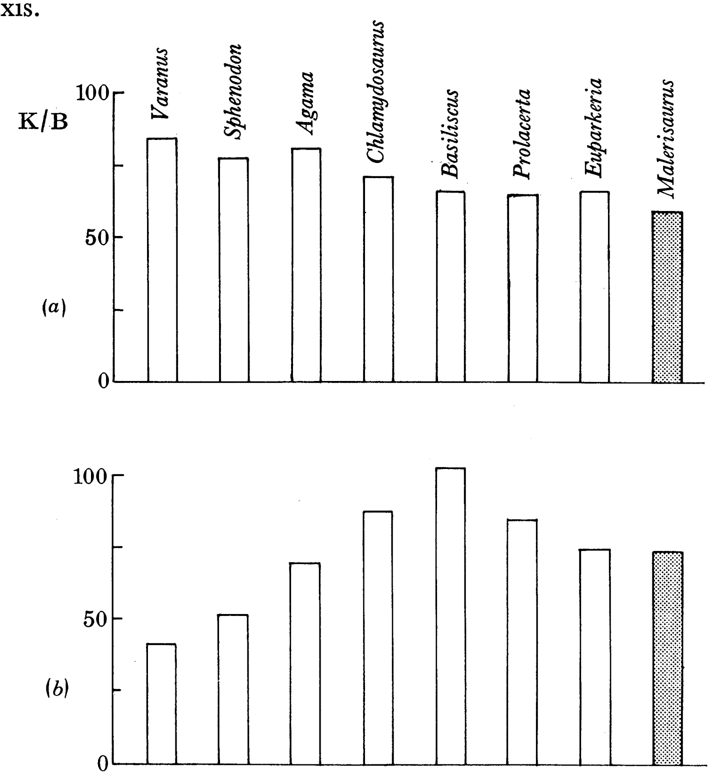


FIGURE 11. Limb proportions of various reptilian genera: (*a*) sum of (humerus + radius) lengths as a percentage of sum of (femur + tibia) lengths; (*b*) sum of (femur + tibia) lengths as a percentage of trunk length. (Adapted from Ewer 1965.)

From the construction of the femur and the acetabulum, the arc of rotation of the femur can be worked out. In protraction the femur lines up with the body without much difficulty, but in retraction the internal trochanter would obstruct the farthest posterior movement. The arc of rotation of the femur is therefore of about 90° when viewed from the top. The femur has a rotary motion, forward and out, backward and in, and its distal end describes an ellipse. The largest and most powerful femoral retractors, the caudifemoralis muscles, lie in the base of the tail. Apart from these, the main muscles responsible for moving the femur are the adductor femoris and ischio-trochantericus femoralis in the power stroke and the pubo-ischio-femoralis internus and ambiens in the recovery stroke.

Since the tibia and pes of *Malerisaurus* are as long as the femur, the stride of the animal must have been very long. During cursorial progression (figure 12), since the hindlimbs could not be drawn under the body but project outward and downward as the pes was implanted, the pes would necessarily be toed-out rather than pointed forward. The mesotarsal joint was effective for speedy locomotion of *Malerisaurus* and, because of the animal's slight weight (about 10 kg), development of a crocodiloid tarsus with a massive calcaneal tuber was unnecessary.

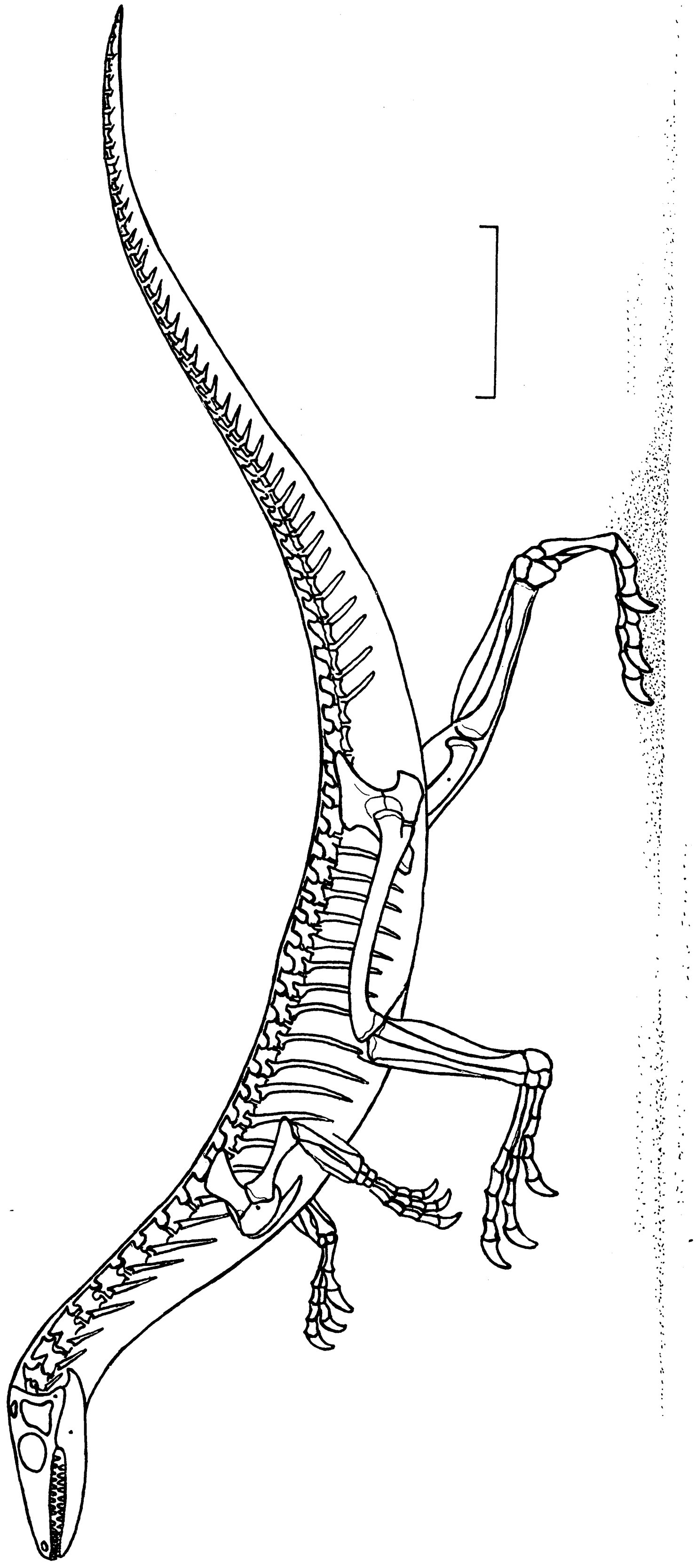


Figure 12. *Malerisaurus robinsonae*, n.sp. Restoration of the skeleton in running posture. Scale bar 15 cm.

7. Palaeoecology

The palaeoecology of the Pranhita–Godavari Valley during the Upper Triassic is partially recorded in the Maleri sediments and its enclosed fossils. The sediments are poorly sorted continental clastics, containing evidence of fluviatile deposition. Red clay is the dominant lithology, usually structureless and unlithified, intercalated with lenses of fine-grained calcareous sandstones and lime-pellet rocks. These lenses, which are cross-bedded and arcuate in plan, are interpreted by Sengupta (1970) as abandoned older channels of a main stream, which were left behind in the interchannel flood plain as cut-off meanders. The finer clay fractions were probably deposited from suspension on the waterlogged flood plains beside the river channel during waning floods.

Red beds and lime-pellet rocks are considered to be good climatic indicators. There are several kinds of red beds (Van Houten 1961), but those lying on the cratons can be roughly divided into two groups: well sorted sediments associated with evaporites; and poorly sorted sediments indicating a fluviatile environment. The Maleri red beds belong to the second category (Robinson 1971). The pigmentation is mainly due to ferric oxide in the form of haematite and the detritals are finely dispersed in the clay. The presence of abundant ferric oxide indicates an alkaline oxidizing depositional environment with warm moist climate and seasonally distributed rainfall. The absence of desiccation cracks, footprints and signs of evaporites indicates that the climate was probably not arid. That this was well watered country, at least seasonally, is suggested by the locally abundant unionids, and by the presence of three aquatic fishes and two semiaquatic tetrapods. The lime-pellet rocks also hint at a subtropical monsoon type of climate, with fairly high year-round temperatures and a dry season alternating with a season of abundant rainfall (Robinson 1964). In essence, the palaeoclimate of the Pranhita–Godavari Valley during Upper Triassic time was not much different from the present-day climate in this region.

There are only a few representatives of the Maleri flora that have been reported; these are mainly petrified wood fragments referable to stem genera *Dadoxylon*, *Araucarioxylon* and *Mesembrioxylon* (Pascoe 1959, p. 976). However, the rarity of plant fossils is probably not the true reflection of the past distribution and density of the Maleri flora. The oxidizing environment which favoured the deposition of haematite in the clay facies was hostile to plant preservation. It is likely that dense forests prevailed in the Maleri landscape, where some of the conifers like *Araucarioxylon* could have been as high as 200 ft (*ca.* 60 m) (Gottesfeld 1972). Beneath this canopy, forest ferns and other low plants formed heavy masses of undergrowth on the forest floor. Certainly there should have been a considerable amount and variety of plants available to supply food and cover for the numerous Maleri reptiles.

The invertebrate fossils are rare in the Maleri rocks; the solitary form known to date is a unionid *Tikhia* (Sahni & Tewari 1958). To this may be added the ostracodes, similar to *Darwinula* and ?Cytheracea, recently recovered from the coprolite sample (Sohn & Chatterjee 1979). The described vertebrates are varied and include the dipnoan fish *Ceratodus*, a pleuracanth shark, a subholostean (Jain *et al.* 1964), a metoposaurid amphibian (*Metoposaurus*) (Roy Chowdhury 1965), a rhynchosaur (*Paradapedon*) (Chatterjee 1974), a parasuchian (*Parasuchus*) (Chatterjee 1978), and the eosuchian *Malerisaurus*. Additionally there are a number of undescribed forms, such as a coelurosaur, a thecodontosaur, an aetosaur (*Typothorax*) and a traversodont (*Exaeretodon*). This list, probably incomplete, certainly attests to the richness of the Maleri fauna.

The vertebrate fossils are invariably abundant in clay facies, indicating that the Maleri fauna consisted essentially of lowland forms that inhabited the flood plains of river valleys and the margins of lakes. The occurrence of *Malerisaurus* in the stomach of *Parasuchus* indicates that the ecological niches of these prey and their predators overlapped somewhat. In spite of careful search in the whole Pranhita–Godavari Valley, I have not found any bones of *Malerisaurus* other than this unusual association. Does this indicate a specialized microhabitat of *Malerisaurus* in the broad water-edge environment?

Bakker (1971) made an interesting correlation between limb proportions and basking behaviour in reptiles. He found that the genera with short limbs usually have the low activity temperatures whereas the long-limbed lizards show high activity temperatures. He concluded that high limb length to body mass ratios seem to be associated with well developed basking behaviour and preference for rather open exposed microhabitats. This may increase the detection of predators, and thus basking species may require limbs capable of higher speeds and more erratic evasive manoeuvres than in less heliophilic species. The gracile body of *Malerisaurus* with its great limb disparity indicates fast, erratic bipedal locomotion with head carried rather high giving good view of terrain. The position of external nares, and the state of ossification of the limbs, carpus and tarsus of *Malerisaurus* indicate a terrestrial life. Zygapophyses are moderately tilted throughout the series, which would prohibit much lateral flexure. Many modern reptiles, such as crocodilians and iguanians, swim by the lateral flexure of the body and tail, clamping their legs to their sides. In *Malerisaurus*, the height of the neural spines decreases rapidly posteriorly, and the end of the tail is a slender whiplash like that of many terrestrial lizards. In those forms with swimming tails, the neural spines are tall for most of the caudal length. Therefore, although *Malerisaurus* probably lived most of its time on a river flood plain or on marshy land near to streams and lakes, it was not well adapted to a true aquatic life.

Many terrestrial lizards, when they are pursued or frightened, take readily to the water, where they swim or dive and hide beneath the surface. This ability would confer an obvious advantage in terms of terrestrial predator avoidance. Probably *Malerisaurus* could swim when occasions demanded. In size and proportion *Malerisaurus* is not far from *Basiliscus*. Possibly younger forms could skitter on the water like the basilisk. The frequent use of aquatic bipedalism in preference to swimming would confer additional advantage in avoiding numerous potential aquatic predators, especially the parasuchians in the Maleri ecosystem (Rand & Marx 1967).

It is worthwhile to examine the possibility of an arboreal habitat for *Malerisaurus* since lightness and agility are of advantage in arboreal adaptation. The humerus seems to have a wide range of brachial movements, because it is longer than the scapula, its head is more medial in position and the deltopectoral crest is proximally placed (Swinton 1936). In most arboreal reptiles, the great limb disparity is a conspicuous feature; so it is in *Malerisaurus*. However, there is always some danger in speculating about the habits of an animal solely from osteological evidence. Thus analogy with modern reptiles is instructive. A similarity of gross anatomy is likely to be correlated with similarity of habitat, locomotion and general way of life. Neill (1971) observed that many of the bipedal iguanians, such as the tamacuaré (*Enyalioides*), striped basilisk (*Basiliscus*), abbess lizard (*Corytophanes*), water dragon (*Physignathus*), sail-sail (*Hydrosaurus*) and frilled lizard (*Chlamydosaurus*), are active climbers. They use tree branches as an escape route as well as for sleeping, basking or hatching. In the Maleri ecology at least three potential predators, coelurosaurs, thecodontosaurs and parasuchians, prevailed. Thus escape into the tree branches from these potential predators would be highly advantageous for *Malerisaurus* when such occasions demanded.

What was the food of *Malerisaurus*? Dental morphology is strongly influenced by selective factors operating through diet and thus provides information regarding the feeding habits of the form in question. The teeth of *Malerisaurus* are of a generalized carnivore type. The lack of serrations indicates that the teeth were not effective for cutting flesh. The anterior teeth are slim, conical and recurved, and thus are suitable for catching small prey. The posterior teeth are large, compressed sideways and show wear facets on occlusal surfaces. Since replacement activity is clear in the jaw, the wear facets indicate that the prey had a hard integument. Most probably *Malerisaurus* consumed beetles, snails and insects as its primary diet. Strong pterygoidal teeth suggest proficiency in crushing hard food.

Many of the present-day lizards rely heavily on insects for food. Hotton (1955) classified three kinds of insect foods consumed by lizards: (1) passive forms, which are subdued by oral secretions of the predators without use of teeth which and are often captured by the tongue; (2) forms of intermediate activity, which must be bitten to be subdued (securing them requires the assistance of teeth, at least in the initial seizure); and (3) active forms, which must be chewed or otherwise injured to some extent to be subdued sufficiently for swallowing. Although no insects are preserved in the Maleri rocks, we know from elsewhere in the fossil record that they must have been abundant and diversified and would have provided an abundant and reliable source of food.

The combination of long limbs and long neck is usually associated with browsing high in shrubs and trees. *Malerisaurus*, as revealed from the dentition, did not show a preference for a vegetable diet. The long neck probably developed as part of a specialized, arboreal, insect-eating mode of life that included slow stalking along narrow branches. A long neck would have given *Malerisaurus* a greater vertical choice of food than that available to shorter-necked forms.

The unique association of prey and predator indicates that each *Parasuchus* died shortly after eating a *Malerisaurus*. Perhaps the preys were poisonous to eat. Does this one-to-one association say anything about social behaviour or gregarious habits among Maleri reptiles? It is often argued that we find lower vertebrates together not because of any social stimulation or attraction from conspecifics, but merely because the place in which they are gathered provides some favourable resources, such as food, nest sites or desirable micro-climatic features. Reptiles are often considered to be dumb, dull and machine-like, having an extremely limited and uninteresting life style. The popular view is that except when mating reptiles engage virtually no intraspecific interactions. This view has recently been seriously challenged by Burghardt (1977). He showed, even among neonate reptiles, a number of diverse types of social behaviour and communication processes, such as (1) vocalization in crocodilians, (2) synchronized nest emergence, migration and foraging behaviour in iguanians, (3) aggregation behaviour in snakes and (4) dominance in turtles. He concluded that the generalized reptilian level of social organization may not be as inferior to that found in birds and mammals as is usually believed. Ostrom (1972) also inferred, from the preferred orientations of trackways, that at least some of the dinosaurs were probably gregarious. It is likely that Maleri reptiles also participated in some group-coordinated activities (such as foraging, escaping, or selecting sleeping and nesting site) and concomitant communicatory processes (figure 13).

Figure 13. *Malerisaurus robinsonae*, n.sp. (one-tenth natural size). Life restoration of two skeletons in running posture, showing quadrupedal and bipedal gaits.

8. The affinities of *Malerisaurus*

Problem of classification

Any attempt to estimate the relationship of *Malerisaurus* is much encumbered by the incomplete nature of the skull, as well as by confusing systematics of the related group of reptiles. The skull bones of *Malerisaurus* were disarticulated and jumbled together, and the surface of the elements was poorly preserved. Despite the difficulty of precise restoration, the skull fragments are significant in providing the clues to the configuration of the temporal openings. It is concluded from the previous discussion that *Malerisaurus* is a diapsid where the lower temporal arcade is complete and the quadrate is fixed. The well preserved postcranial skeleton is sufficiently distinctive to indicate its general phylogenetic position.

While *Malerisaurus* is a gracile, long-necked animal with a facultative biped posture, it had not progressed very far from the basal diapsid stock, even in the late Triassic. The retention of the palatal teeth, absence of antorbital and lateral mandibular fenestrae, unossified laterosphenoid, braincase movable in relation to the skull roof, primitive plate-like pelvis with imperforate acetabulum, two separate sacral vertebrae, 'tetrahedral' humerus, femur with terminal head showing large internal trochanter and mesotarsal ankle joint collectively indicate that its structural grade of organization is most comparable to that of the primitive order of Eosuchia of the subclass Lepidosauria.

Although eosuchians have long been recognized as the stem order from which arose such important groups as rhynchocephalians, squamates and archosaurs, their classification, interrelationships and phylogeny are highly confused. New discoveries and recent interpretation have prompted much work on this topic. Romer (1956) recognized four suborders within Eosuchia: Millerettiformes, Younginiformes, Choristodera and Thalattosauria. A number of enigmatic reptiles from late Permian of Germany (*Protorosaurus*) and from marine Triassic deposits of Tessin Alps (*Macrocnemus* and *Tanystropheus*), unknown almost anywhere else, have been difficult to place in proper categories, mainly because of incomplete knowledge of cranial structures. Kuhn-Schnyder (1962, 1967) suggested that these aberrant genera are actually diapsid, similar to *Prolacerta*, and grouped them in the family Prolacertidae. This placement has a considerable merit for expressing eosuchian relationship. Romer (1966) concurred with Kuhn-Schnyder and thus erected a suborder Prolacertiformes to accommodate these genera, except *Protorosaurus*, within the Eosuchia; *Protorosaurus* he maintained as a euryapsid. He also transferred millerettids to Cotylosauria from Eosuchia.

The taxonomic position and phylogenetic significance of *Protorosaurus* have been controversial for more than a century. The genus *Protorosaurus* from the late Permian Kupferschiefer of Germany was founded by Meyer (1830). Seeley (1888) described the type skeleton with a restoration, and considered it as a diapsid. Von Huene (1926) also studied the genus and he produced a modified restoration of the skull without any lower temporal opening. Peyer (1937) noted a great number of similarities with *Macrocnemus*, especially in the postcranial skeleton. Camp (1945) concluded that *Protorosaurus*, the type genus of the order Protorosauria, is not, as generally believed, related to *Araeoscelis*, but is an eosuchian closely related to *Prolacerta*. He thus preferred to substitute the ordinal name Protorosauria for Eosuchia as a senior synonym. Romer (1947), answering Camp, maintained that *Protorosaurus* is similar to *Araeoscelis*. Vaughn (1955) supported Camp in allying *Protorosaurus* with other eosuchians. Von Huene (1956), Watson (1957) and Tatarinov (1964) noted many prolacertilian features in *Protorosaurus*.

Later Romer (1966) compromised and avoided the ordinal name Protorosauria, but used Araeoscilidia, following Tatarinov. He, however, grouped *Protorosaurus* with *Araeoscelis* in Araeoscilidia. A detailed study of *Protorosaurus* is very much needed, especially an X-ray study of the sole skull, housed in the Royal College of Surgeons in London, to resolve this dilemma. In spite of the incomplete nature of the skull, the postcranial skeleton of *Protorosaurus* is so similar to that of other eosuchians that there is no doubt about their phylogenetic relationship. *Protorosaurus* is considered here as a member of the suborder Prolacertiformes of the order Eosuchia.

Carroll (1977) demonstrated that various eosuchian genera of the family Paliguanidae (Upper Permian) are actually ancestral lizards. He suggested (Carroll 1976*a*) that *Noteosuchus*, usually considered as a eosuchian, is actually the earliest rhynchosaur. He further pointed out (Carroll 1976*b*) that the advanced younginid *Heleosaurus* is ancestral to archosaurs. Carroll was thus able to sort out some of the genera from the 'catch-all' order Eosuchia. Similarly Gow (1975) showed that *Youngina*, which has been considered as central to the eosuchian concept, is already specialized with the development of scutes (unknown in other eosuchians), and thus he questioned its eosuchian affiliation. It is beyond our scope to discuss the relationship of various eosuchian genera. Our discussion will be centred on the Prolacertiformes and their allies, as *Malerisaurus* shows the closest resemblance to this group.

Even so, the problem of classification is not easy. *Prolacerta*, the type genus of Prolacertiformes, has been considered as ancestral to squamates because of its breakdown of the lower temporal arcade, atrophied quadratojugal, and streptostylic quadrate (Parrington 1935; Robinson 1967). A contrasting view has been postulated by Gow (1975). He, on the basis of new material, gave an excellent description of *Prolacerta* and a stimulating discussion of its relationships. He suggested that *Prolacerta* and *Pricea*, both known from the same horizon of South Africa, are congeneric, the former name being the valid one. He then bracketed *Prolacerta* with *Macrocnemus* in a family Prolacertidae, and transferred *Tanystropheus* into a separate family Tanystropheidae. He regarded these two families as sterile offshoots from eosuchians, which paralleled squamates in the loss of the lower temporal arcade, although they are not actually related to true lizards. However, when he discarded the concept of Prolacertiformes and erected a new order Parathecodontia (subclass incertae sedis) for grouping these two families, his argument is not entirely convincing. He argued that *Prolacerta* and *Proterosuchus* show similar skeletal morphology and thus considered *Prolacerta* and allied forms as thecodonts in 'almost every respect'. We have to remember that *Proterosuchus* is the most primitive thecodont, little developed beyond the eosuchian grade (Hughes 1963; Cruickshank 1972). *Prolacerta* and *Proterosuchus* are contemporaneous, both being known from the Lower Triassic *Lystrosaurus* zone, and thus a sharing of primitive characters between these two genera is not unexpected. Even so, each genus shows different styles of radiation: *Prolacerta* by breaking down of the lower temporal arcade, and *Proterosuchus* by the development of an antorbital fenestra. The latter feature is the unique archosaurian hallmark, and its absence in *Prolacerta* clearly indicates that it had not attained the proper thecodont grade. Other specializations of *Proterosuchus* include heavily built quadrupedal posture, downturned premaxillae, serrated teeth, less elongated cervicals, procoelous dorsals, heavier girdles, interclavicle and ilium having distinctive shapes, and the exclusion of the pubis from the acetabulum. Similarity between these two genera extends to the unossified laterosphenoid, limb structures, plate-like pelvis and the retention of intercentra. These similarities may be attributed purely to a common inheritance of primitive characters. Since there appears to be little or no positive evidence that *Prolacerta* (and its allies) are related to thecodonts, as Gow claimed, it seems reasonable to continue the subordinal term Prolacertiformes for them.

Wild (1973) recently gave a detailed description of *Tanystropheus* with a new restoration of the skull that shows clearly that the lower temporal arcade of this genus is lost. He thus considered *Tanystropheus* as a true lizard. Later Kuhn-Schnyder (1974) agreed with Wild's diagnosis and included *Macrocnemus* in the lizard category. However, the loss of the lower temporal arcade may not necessarily be indicative of lizard affinity. Clearly this feature evolved independently in many lepidosaurs, such as *Prolacerta*, as well as in the sphenodontid *Glevosaurus* (Robinson 1973), and may be related to special feeding adaptation. Carroll (1977) pointed out that, in all Permo-Triassic and Jurassic lizards, small body size is the distinctive feature. In the postcranium, cervicals are short, an ossified sternum is present, the scapulo-coracoid shows anterior fenestration, and a thyroid fenestra can be seen in the pelvis. None of these lacertoid tags, except for the thyroid fenestra, is present in either *Tanystropheus* or *Macrocnemus*. Moreover the adult *Tanystropheus* could be as long as 6 m. Carroll thus doubted the lacertoid affinity of *Macrocnemus* and *Tanystropheus*. It is thus obvious from the above discussion that Romer's Prolacertiformes is the only choice for grouping these enigmatic reptiles.

Recently Olsen (1979; Olsen *et al.* 1978) reported a new tanystropheid, *Tanytrachelos*, from the late Triassic Newark supergroup of the eastern United States. This is a small gracile reptile, about 20 cm in length, with the neck as long as the trunk. The new genus can be distinguished from *Tanystropheus* by its small size, long limbs and relatively short cervicals which show ploughshare-shaped ribs posteriorly. Olsen pointed out that *Gwynnedosaurus*, tentatively included by Romer (1966) within Prolacertidae, could be a lizard, as the scapulocoracoid shows anterior emargination. On the other hand, Olsen questioned the avian affinities of *Cosesaurus*, known from the Upper Muschelkalk of Spain (Ellenberger & Villalta 1974; Melendez 1977), because of its problematic feather impressions. He considered *Cosesaurus* as a tanystropheid. Because of a lack of good descriptions and illustrations it is very difficult to ascertain the systematic position of *Cosesaurus* at present.

T. Roy Chowdhury (personal communication) has discovered a very interesting prolacertid from the middle Triassic Yerrapalli Formation of India. It is a gracile quadruped with a small skull and an extremely long neck. The naris is confluent, the quadratojugal is atrophied with loss of lower temporal arcade and the quadrate is streptostylic. In general, the new Yerrapalli form is very similar to *Prolacerta*, though the former is much larger in size, and exhibits an extremely elongate neck, reminiscent of that of *Tanystropheus*.

Comparison of *Malerisaurus* with *Trilophosaurus* proves instructive. *Trilophosaurus* is known fairly completely from the late Triassic Dockum Group of Texas (Gregory 1945). This is a bizarre reptile of uncertain relationships in which the skull is highly specialized. The skull is deep and massive with only an upper temporal opening present. The animal was stoutly built with short neck and well developed limbs. Specialized dentition includes a toothless beak, presumably horn-covered; the cheek teeth were transversely broadened and bear three cusps. The quadrate is tall and fixed with a highly developed otic notch. The centra are procoelous in the cervicals and caudals and platycoelous in dorsals; intercentra are present throughout the column, and the cervical ribs are fused to transverse processes. These are the visible contrasts with *Malerisaurus*. However, when the limbs and girdles are compared, *Trilophosaurus* and *Malerisaurus* show strong resemblances.

Gregory put *Trilophosaurus* within Protorosauria (=Araeoscelidia) on the basis of the single upper temporal opening. He found similarities between *Trilophosaurus* and so-called protorosaurs such as *Protorosaurus*, *Macrocnemus*, *Tanystropheus* and *Araeoscelis*, of which the first three genera are now regarded as diapsids. He (p. 306) admitted that '*Trilophosaurus* is more closely related to the Lepidosauria than to any other group'. He agreed that the edentulous beak and the transversely widened teeth in *Trilophosaurus* may be secondarily adaptive characters related to a specialized chewing habit and are no bar to relationship to other groups. Thus, except for the single temporal opening, there is no notable comparison between *Trilophosaurus* and *Araeoscelis*. The proper classification of *Trilophosaurus* depends on whether this species is directly derived from a diapsid and has secondarily closed up the lower temporal opening. This is not uncommon among diapsids. In ankylosaurs, only the upper temporal opening is closed (Romer 1956), whereas in *Scleromochlus* both temporal openings are closed (Walker 1970). It seems logical to include *Trilophosaurus* within the Lepidosauria, possibly as a sterile offshoot from the rhynchocephalian lineage. Acceptance of *Trilophosaurus* as a lepidosaur leaves *Araeoscelis* as the sole member of the order Araeoscelidia. *Araeoscelis* could be grouped with the captorhinomorphs, as Vaughn (1955) concluded after a lengthy discussion, in the same way that Romer (1966) bracketed the millerettids with the procolophonids, refusing in each case to treat a single character, the temporal opening, as all-important in the classification of reptiles.

We have thus far restricted our discussion to the Prolacertiformes and their allies. The question is often asked: if the eosuchians are central to later diapsid radiation, from what group did the eosuchians evolve? The oldest known diapsid, *Petrolacosaurus* (Peabody 1952), from the Upper Pennsylvanian of Kansas, is the ideal ancestor for the Permian diapsids. Surprisingly *Petrolacosaurus* shows a greater degree of similarity with the Prolacertiformes than with any other group of eosuchians, especially in the development of an elongate neck and gracile body. Peabody included *Petrolacosaurus* in a distinct family Petrolacosauridae within the Eosuchia. Romer (1956) doubted its diapsid nature as the temporal region of this genus was then poorly known, and he provisionally placed it within the synapsids. However, from the recent work of Reisz (1975, 1977) on the basis of better material, it becomes clear that *Petrolacosaurus* is a true diapsid and bridges the morphologic gap between the stem reptile family Romeriidae and eosuchians.

Evolutionary development

Comparison of *Malerisaurus* with other Prolacertiformes offers more positive evidence of probable relationships. Several skeletal features that appear to be little, if at all, advanced, over the earliest member *Petrolacosaurus* are as follows (figures 14, 15):

(1) skull narrow and elongate, slender jaws, large orbit;
(2) marginal teeth conical and subthecodont;
(3) palatal teeth persist;
(4) tall quadrate;
(5) large palatal fenestra;
(6) large post-temporal fenestra;
(7) retention of coronoid;
(8) elongated cervicals with extended zygapophyses, midventral keels and low appressed diapophyses;
(9) amphicoelous centra, two separate sacral vertebrae;
(10) dichocephalous ribs;
(11) plate-like pelvis with imperforate acetabulum;

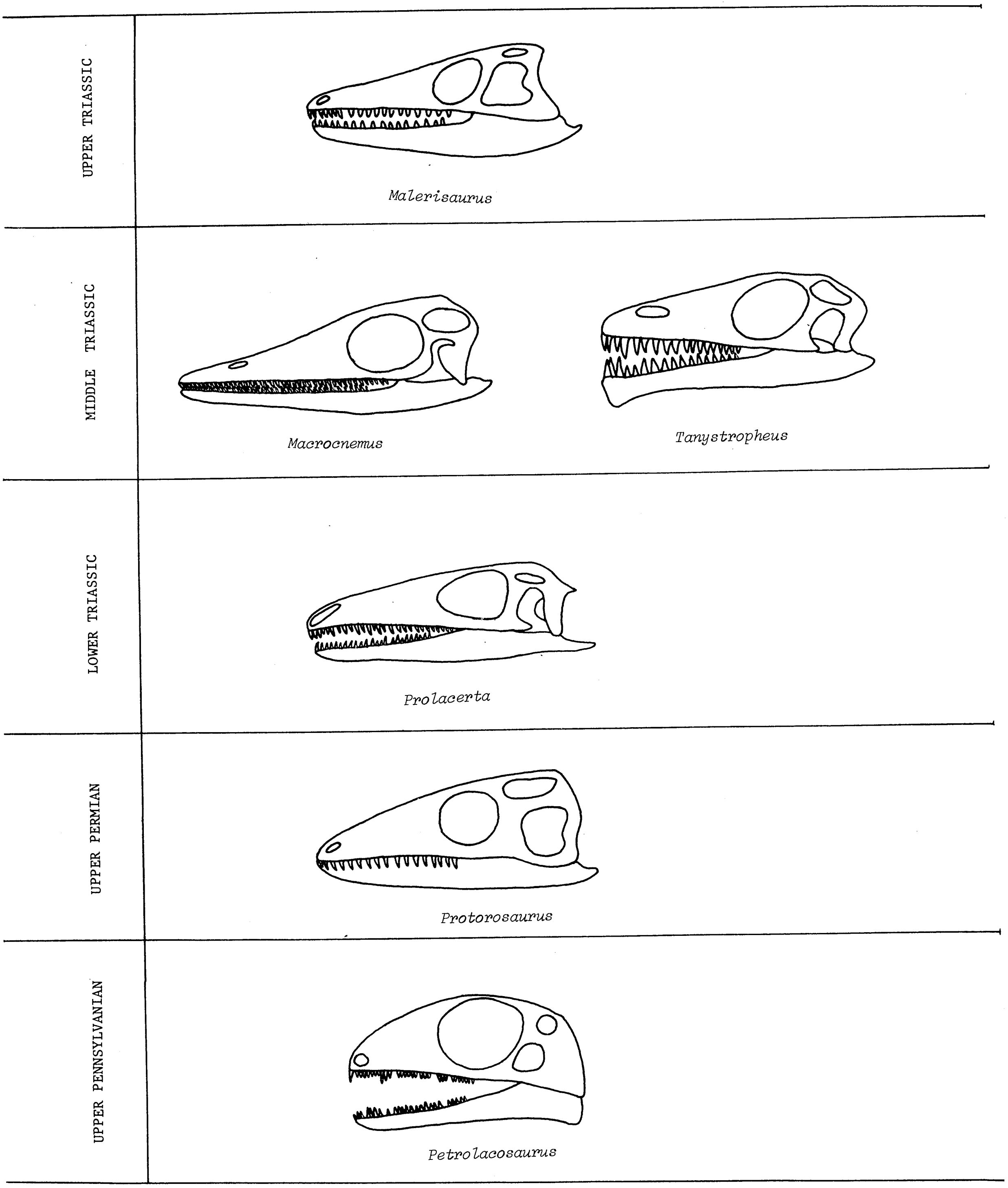


FIGURE 14. A comparison of the skull of the different genera of Prolacertiformes: *Petrolacosaurus* (after Reisz 1977); *Protorosaurus* (modified from Seeley 1888); *Prolacerta* (Gow 1975); *Macrocnemus* (Kuhn-Schnyder 1967); *Tanystropheus* (Wild 1973).

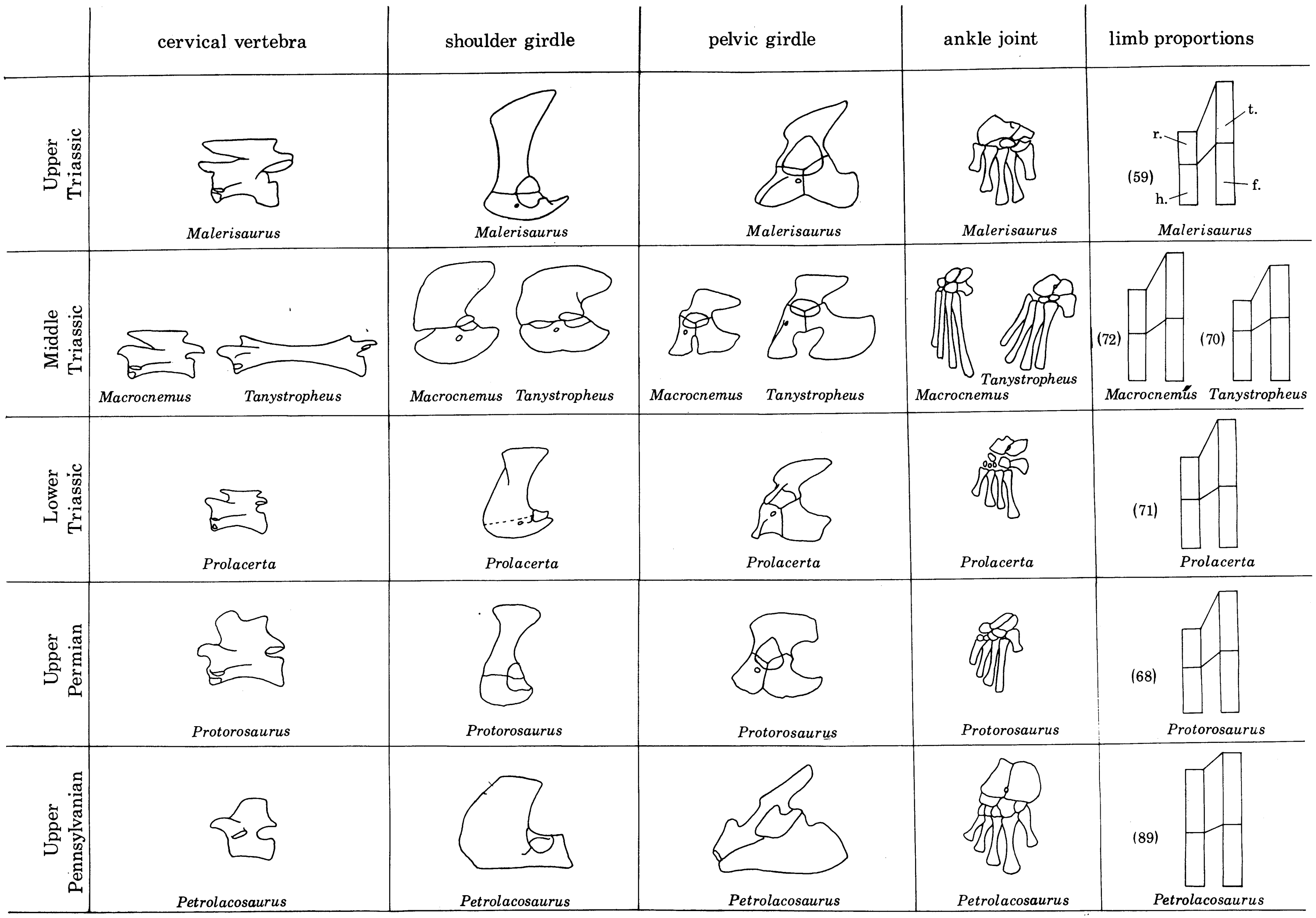


FIGURE 15. A comparison of the postcranial of different genera of Prolacertiformes. *Petrolacosaurus* (after Peabody (1952) and Reisz (1975)); *Protorosaurus* (Peyer 1933; von Huene 1926); *Prolacerta* (Gow 1975); *Macrocnemus* (Peyer 1933); *Tanystropheus* (Wild 1963). In the right column the forelimb:hindlimb ratio is shown; femur length is taken as unity; the number in parentheses indicates limb-proportion index, i.e. sum of lengths of (humerus (h.)+radius (r.)) as a percentage of the sum of the lengths of (femur (f.)+tibia (t.)).

(12) slender limbs, tetrahedral humerus;
(13) femur with prominent internal trochanter;
(14) mesotarsal ankle joint, large astragalus and calcaneum.

The retention in *Malerisaurus* of such a large number of primitive eosuchian traits supports the contention that this reptile is derived from early eosuchians. From the primitive *Petrolacosaurus*-like ancestor, the progressive morphologic changes of *Malerisaurus* could be traced by the following evolutionary development:

(1) reduction of marginal teeth;
(2) loss of post-temporal bones;
(3) reduction of palatal teeth;
(4) loss of parietal foramen;
(5) improvement of middle ear for airborne sound transmission;
(6) elongation of cervical neural spine to the length of the centrum;
(7) extension of the posterior process of the ilium;
(8) increase of limb disparity;
(9) femur became slender and sigmoidal;
(10) loss of epicondylar foramen in humerus;
(11) loss of centrale and distal tarsals 1 and 2.

Phylogenetic relationships

There seem to be two distinct phyletic lines among the different genera of Prolacertiformes on the basis of the configuration of the lower temporal opening. In one group, containing, for example, *Petrolacosaurus*, the lower temporal arcade is complete; in the other, as exemplified by *Prolacerta*, the lower temporal arcade is breached. What was the nature of the lower temporal opening, if any, of *Protorosaurus*? We do not know. But from Seeley's (1888) restoration and description of the quadrate, it appears that the lower temporal arcade of this genus was probably not lost, a condition that could have led to *Malerisaurus*. Both *Protorosaurus* and *Malerisaurus* are thus tentatively grouped within the Protorosauridae, with the assumption that the lower temporal arcade remained intact in these two genera similarly to that of *Petrolacosaurus* with a fixed quadrate. This implies a long hiatus of the fossil record within this family between the late Permian and the late Triassic, and future discovery may fill this important gap. *Petrolacosaurus*, however, is placed in a separate family Petrolacosauridae because of the primitive middle ear region, insensitive to airborne sounds (Peabody 1952; Reisz 1977).

In the rest of the genera, progressive evolution can be seen in a separate phyletic line. Here the lower temporal arcade was breached, the quadratojugal was atrophied or lost, and the quadrate became streptostylic. In this lineage we follow Gow's (1975) classification, recognizing two separate families: Prolacertidae (including *Prolacerta*, *Macrocnemus* and the new Yerrapalli form); and Tanystropheidae (including *Tanystropheus* and *Tanytrachelos*). The latter could be further differentiated by the greatly elongate neck and by heterodonty in the juvenile form. The inferred phylogenetic relationship may be represented by the following diagram (figure 16).

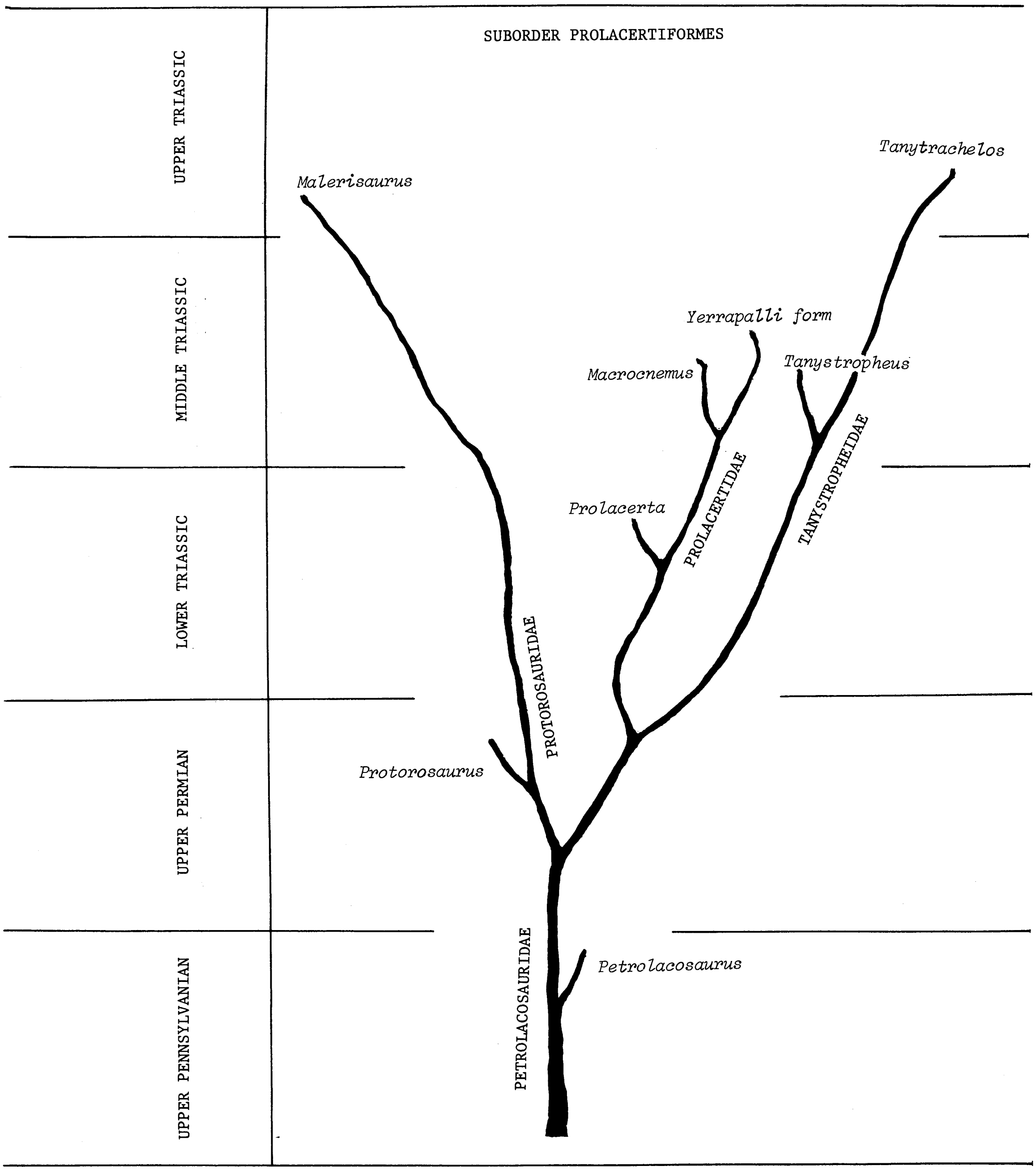


FIGURE 16. Suggested phylogeny of the different genera of Prolacertiformes.

Outline of classification

order Eosuchia Broom, 1914
diagnosis as in Romer (1956, p. 519)
suborder Prolacertiformes Camp, 1945

Gracile eosuchians of small (18 cm) to moderate (6 m) size, with elongate neck and body, long and slender limbs; skull narrow and slender, subterminal nares, large orbit; marginal dentition conical and subthecodont, palatal teeth persist; tall quadrate, streptostylic in some forms; primitive limbs and girdles, no dermal armour; late Pennsylvanian–late Triassic.

family Petrolacosauridae Peabody, 1952

Most primitive member; lower temporal bar complete with fixed quadrate. Primitive features include: palatal teeth on parasphenoid, intercentra throughout the series, middle ear insensitive to airborne sounds, and epicondylar foramen in humerus, stout femur.

genus: *Petrolacosaurus* Lane, 1945
type species: *Petrolacosaurus kansensis* Lane, 1945
Konemo Series, Kansas, U.S.A.; late Pennsylvanian
diagnosis as for the family

family Protorosauridae Lydekker, 1888

Lower temporal arcade probably complete with fixed quadrate; improved middle ear region sensitive to airborne sounds; great limb disparity.

genus: *Protorosaurus* Meyer, 1830
type species: *Protorosaurus speneri* Meyer, 1830
Kupferschiefer, Thuringia, Germany; late Permian

Intercentra present; narrow parietal sagittal crest; posterior process of the ilium not extended, centrale and distal tarsals, first to fourth retained.

genus: *Malerisaurus*, n.gen.
type species: *Malerisaurus robinsonae*, n.sp.
Maleri Formation of central India, late Triassic

Advanced form, posterior teeth slightly heterodont; loss of intercentra, centrale and distal tarsals 1 and 2; ilium extended posteriorly

family Prolacertidae Parrington, 1935

Lower temporal arcade lost, quadrate streptostylic and quadratojugal reduced or lost.

genus: *Prolacerta* Parrington, 1935
type species: *Prolacerta broomi* Parrington, 1935
Lystrosaurus zone, Karroo, South Africa, early Triassic

Large girdles unfenestrated; jugal spar and quadratojugal present.

genus: *Macrocnemus* Nopcsa, 1930
type species: *Macrocnemus bassanni* Nopcsa, 1930
Grenzbitumenzone, Monte San Giorgio, Tessin, Switzerland; middle Triassic and Higher Bunter of Germany (Ortlam 1967).

Girdles reduced, thyroid fenestra in pelvis, quadratojugal absent, slightly hooked fifth metatarsal.

genus: *undescribed* (T. Roy Chowdhury, personal communication, 1979)
Yerrapalli Formation of central India, middle Triassic

Large form, confluent nares, rod-shaped quadratojugal, extremely long neck.

family Tanystropheidae Gervais, 1858

Skull similar to Prolacertidae but with heterodonty in juveniles, showing tricuspid posterior teeth; extremely long neck with 12 cervicals.

genus: *Tanystropheus* Meyer, 1855
type species: *Tanystropheus conspicuus* Meyer, 1855
Grenzbitumenzone, Monte San Giorgio, Tessin, Switzerland, and Besano, Italy; Muschelkalk and Higher Bunter of Germany (Ortlam 1967); Lower Muschelkalk, Gorny Slask, Poland; Wadi Ramon, Israel; middle Triassic.

Very large form, adult may be as long as 6 m.

genus: *Tanytrachelos* Olsen, 1979
type species: *Tanytrachelos ahynis* Olsen, 1979
Newark supergroup, U.S.A., late Triassic.

Small, about 20 cm long, short cervicals with ploughshare-shaped ribs and long limbs.

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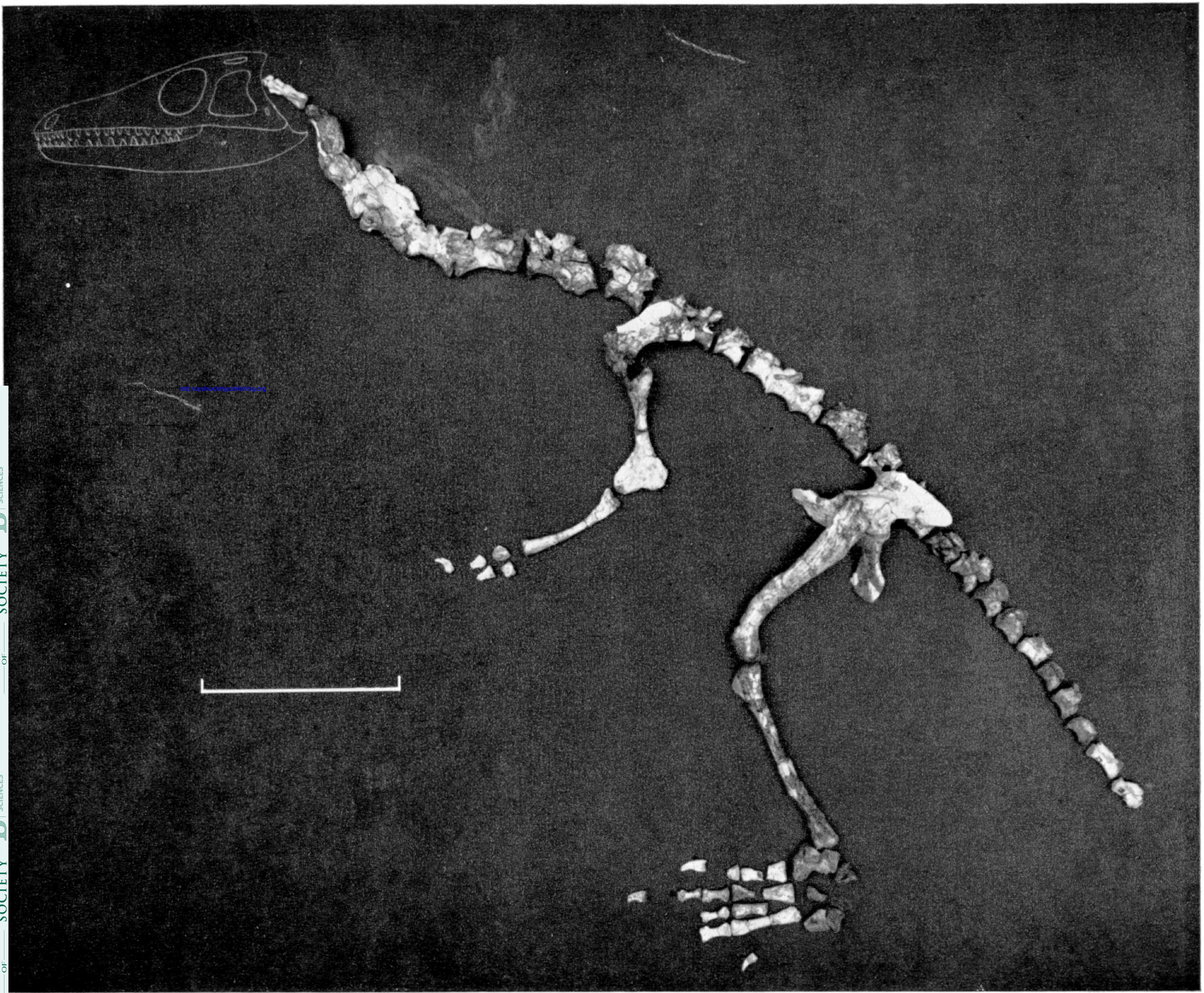

PLATE 1. Postcranial skeleton of *Malerisaurus robinsonae*, n.sp.; specimen ISIR 151; scale indicates 10 cm.