A LATE UPPER TRIASSIC SPHENOSUCHID CROCODILIAN FROM WALES

by P. J. CRUSH

ABSTRACT. The fossil material of a 760 mm long crocodilian, *Terrestrisuchus gracilis* gen. et sp. nov., from a late upper Triassic fissure filling in the Carboniferous limestone of the old Pant-y-ffynon quarry near Cowbridge, Glamorgan, is described. The quadratojugal is parallel sided and the squamosal lacks a descending process. A hard secondary palate is formed by the maxillae and premaxillae. A fenestra pseudorotundum is present but the pterygoids were not sutured to the braincase. The Eustachian tubes were ramified. A prearticular is present. The teeth are recurved, flattened, and bear serrations. The ischium projects posteriorly and the pubis, bearing an obturator foramen, borders the open acetabulum. The postero-ventrally extended coracoid joins the ossified sternum. The carpals and tarsals are crocodilian. The fifth metatarsal is reduced but bears two phalanges. The dorsal vertebrae are primitive. A paired row of leaf-shaped dorsal scutes were present. The earliest crocodiles are placed in three suborders—Protosuchia, Sphenosuchia, and Triassolestia. The genus *Pedeticosaurus* is included in the Protosuchia which were ancestral to the Mesosuchia. *Dibothrosuchus*, *Hesperosuchus*, *Hemiprotosuchus*, *Pseudohesperosuchus*, and *Sphenosuchus* form part of the Sphenosuchia. *Saltoposuchus* and *Terrestrisuchus* belong in a new family Saltoposuchidae. *Triassolestes* and *Hallopus* are included in their own suborders. The Hallopoda, Sphenosuchia, and Triassolestia have no known descendants.

THE matrix-bearing *Terrestrisuchus*, and five other species of reptile, was found by Professor K. A. Kermack and Dr. P. L. Robinson in the spring of 1952 (Kermack 1956; Robinson 1957*a*). The material was discovered on a tip in the old Pant-y-ffynon quarry, near Cowbridge, Glamorgan. The fossils came from a fissure, of unknown location, in the Carboniferous limestone of the quarry. The finely preserved and abundant material of *Terrestrisuchus* consists primarily of a number of blocks bearing associated and, sometimes, articulated bones but, in addition, there are a large number of individual bones that have been entirely freed from the matrix. The referral of the individual bones to *Terrestrisuchus* can be easily done on the basis of the articulated material. The fossils were prepared out mechanically using a needle mounted in a pin chuck and sharpened with a fine-grade oilstone. The bone was strengthened with dilute poly-butyl-methacrylate lacquer.

Age of the Welsh crocodile. Robinson (1957*a*, *b*) split the vertebrate-bearing fissures of the Bristol Channel area into two groups. The first group yielded mammals or mammal-like reptiles and she aged these as Rhaetic or lower Liassic. The second group, including Pant-y-ffynon, lacked these animals and were believed to be Triassic and pre-Rhaetian. In making this distinction she assumes the older fissures to have been covered by the marine transgression of the Rhaetic. Robinson aged the older fissures on the basis of: a theoretical consideration of the mechanism of formation and filling of the fissures, a detailed consideration of the structure of the fissure at Emborough quarry, and the lack of mammals. Her general interpretations cannot be proven but the fauna of Emborough is shown to have been pre-Rhaetic as Rhaetic deposits covered this quarry. Robinson (1971) aged the Pant-y-ffynon fissure as upper Norian because she assumed it to have passed through the conglomerate that lies above the Carboniferous limestone, which she regarded as Norian. The relationship of the fissure that contained *Terrestrisuchus* to the conglomerate is unknown as, in the new quarry, fissures both pass through and start below the conglomerate. Furthermore there is no evidence that the conglomerate is of Norian age, it could be Rhaetian or even lower Jurassic. There is no Rhaetic covering at Pant-y-ffynon. Faunal correlations between Robinson's Triassic fissures suggest that they are contemporaneous, if the reptiles are assumed to have been evolving rapidly, except for Highcroft

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whose fauna is too poorly known. Furthermore, elements of the fauna of the Triassic fissures are closely related to *Trilophosaurus* (Case 1928*a*, *b*; Gregory 1945), *Icarosaurus* (Robinson 1962; Colbert 1965), and *Saltoposuchus*. *Trilophosaurus* comes from the Dockum beds, *Icarosaurus* from the Locatong facies of the Newark group, and *Saltoposuchus* from the Stubensandstein. *Trilophosaurus* and *Icarosaurus* are usually considered upper Triassic and the Stubensandstein as upper Triassic but pre-Rhaetic. Thus these correlations, and Robinson's age determination of Emborough, imply that *Terrestrisuchus* was upper Triassic and pre-Rhaetian in age.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA
Order CROCODYLIA
Suborder SPHENOSUCHIA
Family SALTOPOSUCHIDAE fam. nov.
Terrestrisuchus gen. nov.

Type species. *Terrestrisuchus gracilis*. sp. nov.

Diagnosis. Small terrestrial crocodilian; skull bones unornamented; skull table rounded; supratemporal and antorbital fenestrae elongated; frontals excluded from supratemporal fenestrae; squamosal large and convex laterally; frontals and parietals paired; postorbital bar superficial; otic notch formed; quadrates bear conchae, slope anteriorly, and buttress under the squamosals; quadratojugal parallel sided; nineteen maxillary teeth; maxillae and premaxillae form a secondary palate; anterior palatal fenestrae present; interpterygoid vacuities present; basipterygoid articulations movable; pterygoids not sutured to the braincase; pterygoid flanges formed; Eustachian tubes ramified; fenestra pseudorotunda formed; external but no internal mandibular fenestra present; prearticular present; no pronounced retroarticular process; articular fenestrated and possessing a dorsally directed, medial, process; teeth thecodont, recurved, flattened, bearing anterior and posterior cristae and serrations; vertebrae platycoelous; neural spines low; about twenty-four presacrals; two sacrals; about seventy caudals; all presacrals bear free ribs; costal articulations fuse only on the last presacral; dorsal ribs bear only anterior flanges; double row of dorsal, ornamented, leaf-shaped scutes; pectoral girdle lacks clavicles; ossified sternum present; slender interclavicle present; coracoids extended postero-ventrally; supracoracoid foramen present; scapula expanded into points anteriorly and posteriorly; limb bones hollow; humerus with a well-developed deltopectorial crest; ulna bears a slight olecranon; carpus crocodilian; only one distal carpal; ilium with pre- and post-acetabular processes; supra-acetabular crest well developed; acetabulum perforated; pubis entered acetabulum; obturator foramen present; ischium projected posteriorly; pelvic symphysis present; femur with a fourth but no lesser trochanter; tarsus crocodilian; metatarsal five reduced but bearing two phalanges; metatarsals one to four subequal in length.

Etymology. The generic name has been chosen in order to emphasize the terrestrial nature of the early crocodiles.

Terrestrisuchus gracilis. sp. nov.

Diagnosis. As for genus. The specific name refers to the light graceful build of this animal.

Holotype. Specimen P. 47/21 and its counterpart P. 47/22. These blocks bear the remains of a single, partially articulated, virtually complete individual. Some bones have been prepared out of these blocks and are labelled P. 47/21a, b, c and P. 47/22a, i. Department of Zoology and Comparative Anatomy, University College, London.

Paratypes. Associated and individual bones. Department of Zoology and Comparative Anatomy, University College London.

Locality and horizon. Fissure filling in the Carboniferous limestone of the old Pant-y-ffynon quarry, about three miles east of Cowbridge, Glamorgan, Wales; late upper Triassic.

DESCRIPTION: SKULL

The identifications of the skull bones were based on the semi-articulated specimen P. 78/1a, the closely associated skull elements on the holotype, and the associated bones on P. 79/1 and P. 147/1. The cranial bones of *Terrestrisuchus* are abundant in the material but unfortunately there are no laterospheroids, prefrontals, premaxillae, or vomers preserved and there is no certain basisphenoid. Of the other elements, there are, on average, between four and five examples of each. There is no evidence for the presence of a dermo-supraoccipital. The restorations are based on an analysis of how the bones articulated with each other. The semi-articulated specimen (P. 78/1a) was of little use in reconstructing the skull as it is incomplete and crushed. The illustrations (text-figs. 1–6) show what is actually known of the bones, their reconstructed form, and their postulated articulations. The basisphenoid was not reconstructed in lateral view (text-fig. 4D, E) and no attempt was made to reconstruct the laterosphenoids. The remains of the quadratojugal have been omitted from text-fig. 1B, the remains of the quadratojugal, parietal, and frontal from text-fig. 2B, and the parietal from text-fig. 4C.

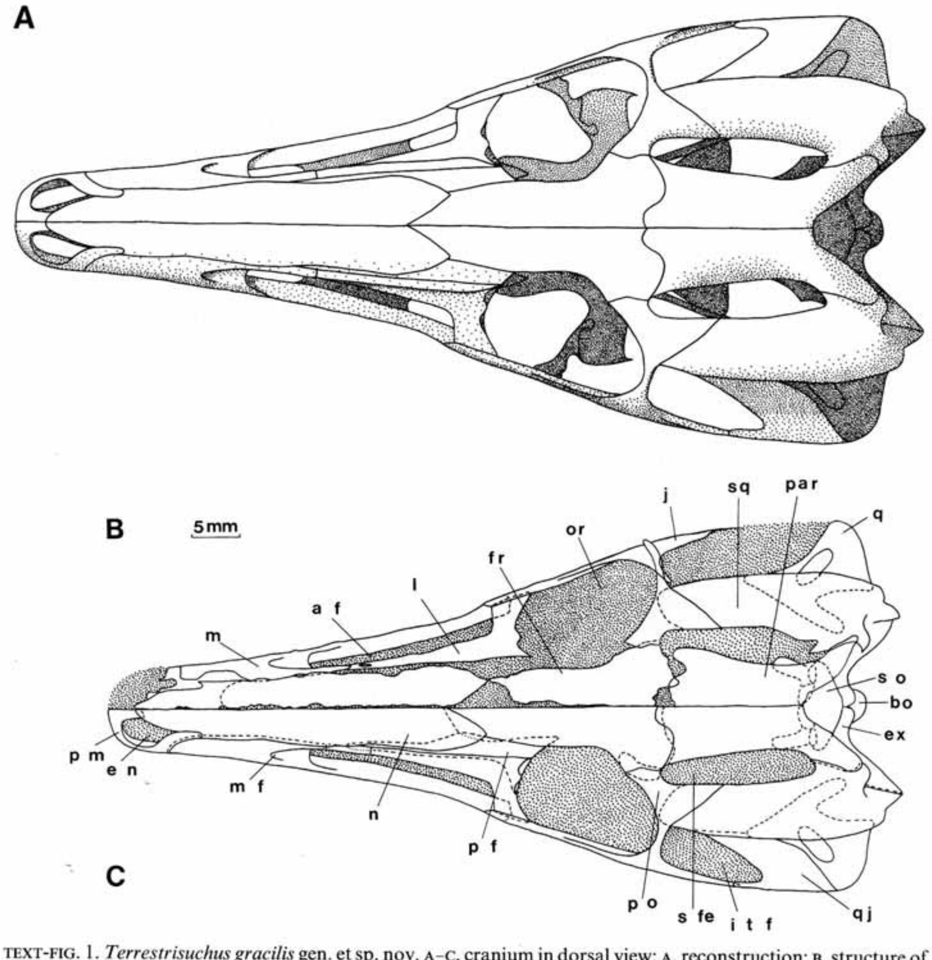
Cranium. The cranium was wedge-shaped in dorsal and lateral views and approximately square in occipital view. The skull table was convex across its longitudinal axis, and the large, flat squamosals sloped strongly ventro-laterally. The postorbital bar was inclined posteriorly. The large, almost centrally positioned, orbit was oval in dorsal view and almost circular in lateral view. The antorbital fenestra, formed by the maxilla and lacrimal, was long and narrow as was the supratemporal fenestra. The infratemporal fenestra, bordered by the broad, parallel-sided quadratojugal, was triangular in outline. The post-temporal fenestrae were large and had a complex shape. The palatal vacuities were approximately oval and long interpterygoid vacuities remain. The basipterygoid articulations were movable. The choanae were elongate oval-shaped openings and a short secondary palate was formed by the premaxillae and maxillae. In life this was possibly extended by soft tissue, across the palatines, to shift the function choanae posteriorly. The quadrate was inclined anateriorly and the otic notch was well developed. The skull did not possess postfrontals or interpterygoids.

Frontal. Eight specimens of the frontals are preserved allowing their complete reconstruction. These bones are paired unlike those of the modern crocodilians which fuse before the animal leaves the egg. The frontals were flat and smooth dorsally with straight medial edges where they sutured together. Anteriorly the dorsal surfaces bear recessed articulations where they were overlapped by the nasals and prefrontals. Posteriorly there were overlapping articulations with the parietals and postero-laterally flanges extended into notches within the postorbitals. There were no articulations between postorbitals and parietals. The ventral surface of each frontal bears a well-developed crista cranil frontale. The anterior part of the orbital surface of the frontal, lateral to this ridge, bore a groove for articulation with the prefrontal. A process was present at the anterior end of the orbital surface which also articulated with the prefrontal.

Jugal. Three examples of this bone are preserved and those on P. 78/1a and P. 79/1a allow this element to be completely reconstructed except for the distal part of the dorsal process. This element is triradiate and consists of anterior, posterior, and dorsal processes. The lateral surface of the bone is smooth. The dorsal process of the jugal is long, slender, slightly tapering, swept back at a small angle to the vertical, and inclined slightly medially. No articular facets for the postorbital are preserved. The postorbital bar was not recessed below the level of the skull surface. The posterior process tapers distally. There is no evidence as to how this bone articulated with the quadratojugal. The anterior process of the jugal is pointed and is constricted centrally. The lateral surface of this process is convex across its length. As only a small amount of the medial surface of the jugal is visible, on P. 78/1a, its articulations with the maxilla, lacrimal, and ectopterygoid, as reconstructed, are purely suppositions.

Lacrimal. Five lacrimals are preserved and together they allow the whole bone to be described. The lacrimal consists of an approximately triangular facial plate and a descending maxillary process. The ventral edge of the facial plate and the anterior edge of the maxillary process bounded the antorbital fenestra. The posterior edge of the maxillary process is slightly concave where it formed the antero-ventral edge of the orbit. The medial surface of the lacrimal is smooth. The postero-dorsal corner of this surface is hollowed out into an approximately triangular recess in which the prefrontal articulated. The prefrontal also fitted within a groove that runs along the dorsal margin of this surface. The medial side of the maxillary process is built up centrally into a low ridge. The opening into the lacrimal duct is positioned just dorsal to the termination of the maxillary process. The lateral surface of the lacrimal was smooth. The anterior end of this surface of the facial plate bore a strong ridge, dorsally, that fitted medial to the maxilla. Details of the ventral articulations with the jugal and maxilla are unknown.

Maxilla. Seven maxillae have been referred to *Terrestrisuchus* and the structure of this bone is almost completely known. The basal portion of the maxilla consists of a long, horizontally orientated, tooth-bearing ramus the ventro-lateral edge of which is nearly straight. Rising dorsally from the anterior half of the basal ramus is an ascending lamina consisting of a facial plate and a postero-dorsally directed projection. The anterior part of the basal portion of the bone is extended medially to form a palatal process. The lateral surface of the maxilla is smooth except for a number of small blood and nervous foramina that run along its ventral margin. A conical fossa is present in the facial plate anterior to the antorbital fenestra. This fossa is directed antero-ventrally and is of moderate depth. The lateral surface of the postero-dorsal projection turns sharply medially and then ventrally where it borders the antorbital fenestra. Articular facets for the nasals are not preserved but it is assumed that they overlapped the dorsal edge of each maxilla. There is no evidence for the mode of articulation with the premaxilla or for a notch between premaxilla and maxilla such as has been figured in *Sphenosuchus* (Walker 1970). The palatal process is rather narrow; it articulated medially with its pair and probably also with the



TEXT-FIG. 1. *Terrestrisuchus gracilis* gen. et sp. nov. A–C, cranium in dorsal view: A, reconstruction; B, structure of the preserved material; C, restoration of the articulations. For explanation of abbreviations, see page 155.

vomers. The posterior edge is concave and formed the anterior border of the internal naries. The maxilla forms the posterior portion of the anterior palatal foramen which opens out from the bottom of a pit that would have been originally formed by maxilla and premaxilla. Specimen P. 144/1 bears oval alveoli for fifteen thecodont teeth and three more were inserted into a common alveolar groove at the back of the maxilla. Specimen P. 147/1a displays the structure of the medial surface of the anterior part of the maxilla. It shows that there was a second ridge running dorsal to the palatal process and separated from the ventral edge of the bone by a groove. It is suggested that this groove bore the chaonal tube and that at least the anterior part of the internal naries were covered by a soft palate.

Maxillary teeth are well preserved on P. 147/a. They have well-developed oval roots and laterally compressed crowns. These teeth are pointed and recurved and bear anterior and posterior cristae which are finely serrated.

Nasal. This bone is well represented in the material and P. 108/1 bears a fine specimen that shows its original outline. The medial edge of the bone is straight where it butt-jointed to its pair. The nasals are pointed anteriorly and posteriorly. The frontals wedged in between them posteriorly and were overlapped by them dorsally. No articular surfaces are preserved for the prefrontals and maxillae. A small process from the anterior end of the bone formed a notch that housed a process of the premaxilla. The dorsal surface of the bone is smooth and whilst it is flat posteriorly anteriorly it becomes strongly convex across its length.

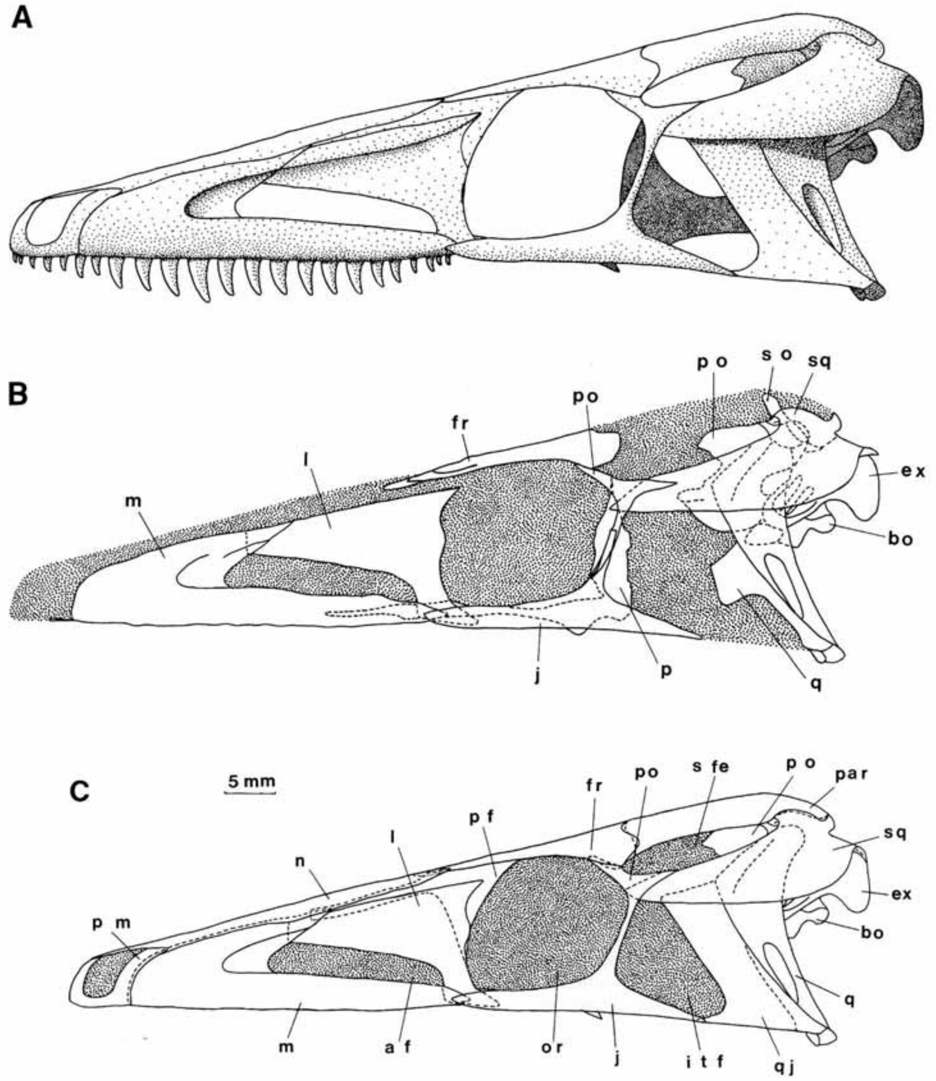
Parietal. Although the six preserved parietals are all in poor condition there is sufficient material to allow this element to be fully described. The parietal is a long narrow bone that articulated with its pair along the midline. Details of this articulation are not preserved but it appears that the bones were simply butt-jointed together. The anterior portion of the lateral edge of this bone formed the gently concave margin of the supratemporal fenestra. The postero-lateral corner of the parietal is extended into a process that articulated with the squamosal and medial to this articulation the bone is deeply notched. It is thought that the supraoccipital joined to the posterior edge of this notch and its anterior processes buttressed against the ventral surface of the parietal but no defined articular facets for the supraoccipital are present. The details of the squamosal articulation are not clear but it is apparent that the postero-lateral process of the parietal fitted into a notch formed for it on the postero-medial edge of the squamosal. The dorsal surface of the parietal is smooth. The centre of the bone is strongly convex across its longitudinal axis which results in the skull table being arched between the supratemporal fenestrae. The edge of the bone dipped steeply into the fenestra and its posterior margin was bent downwards on to the occipital surface.

Postorbital. Only two postorbitals are preserved but the example on P. 79/1c is in excellent condition. This element is a triradiate bone consisting of posterior, lateral, and medial processes. The posterior ramus which overlapped the squamosal is approximately triangular in dorsal view and antero-medially formed part of the margin of the supratemporal fenestra. The lateral process is slender and tapers towards its tip where it articulated with the jugal. The medial process is excavated by a deep groove which housed a process of the frontal.

Prefrontal and premaxilla. No prefrontals or premaxillae have been identified in the material. They have been reconstructed on the basis of the articulations, preserved for them, on the other cranial bones and on the structure of this element in *Sphenosuchus* (Walker 1972). No restoration of the portion of the prefrontal within the orbit has been attempted.

Quadratojugal. The quadratojugal is a very thin, fragile bone and is thus poorly preserved. Two specimens display parts of this element and from these parts, and knowledge of the adjacent bones, the whole can be reconstructed. The quadratojugal has been restored as an approximately parallelogram-shaped bone that increases in width ventrally. The posterior, dorsal, and ventral edges of the bone were straight but the anterior edge was concave. The dorsal edge buttressed under the squamosal but no details of this articulation are preserved. Postero-ventrally the quadratojugal overlapped the lateral edge of the quadrate whilst dorsally it articulated with the thin anterior edge of that bone.

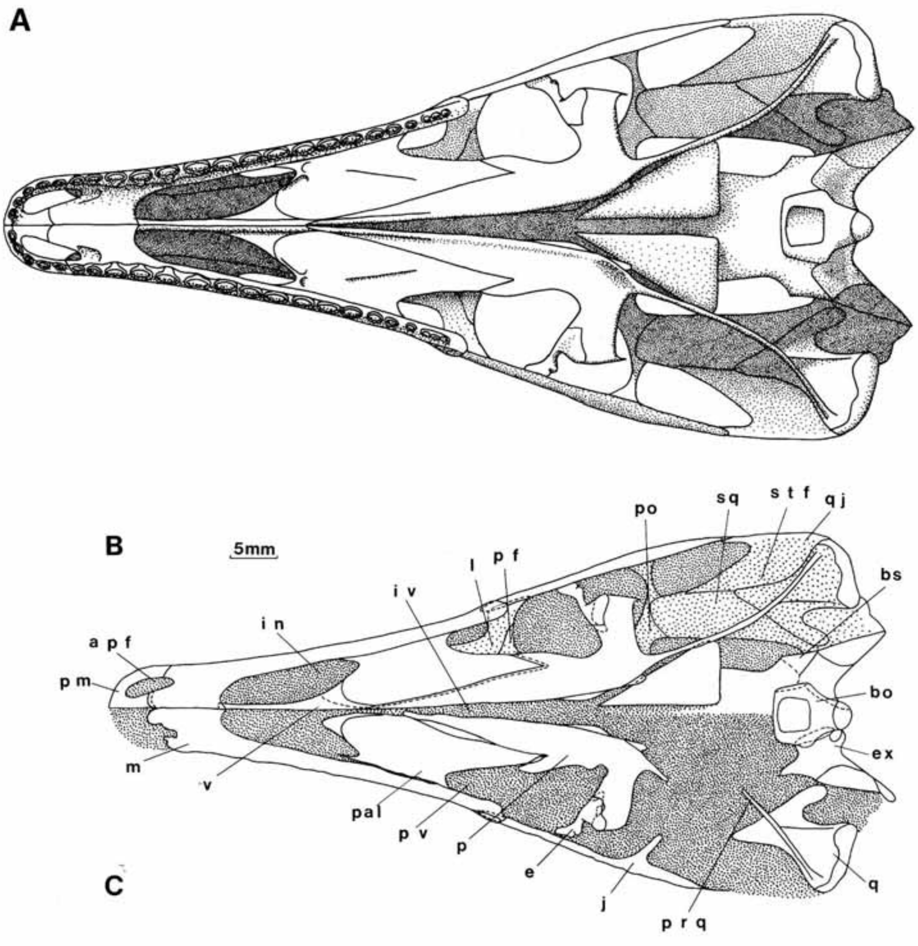
Squamosal. Eight examples of this bone are preserved and its structure is completely known. When viewed directly, the squamosal is approximately flat and kidney-shaped with three posteriorly placed projections. In life its dorsal surface sloped strongly ventro-laterally. This surface is smooth and slightly convex across its length. The lateral edge of the squamosal is convex whilst the medial is concave where it bordered the supratemporal fenestra. The bone surface dipped very steeply into the fenestra. A number of shallow, longitudinal grooves are present on the region of the bone which was overlapped by the postorbital. The largest of the processes of the squamosal extended posteriorly and slightly ventrally. This process articulated with the exoccipital but it is not known how. Medial to this exoccipital process are two more that formed a notch for the postero-lateral process of the parietal.



TEXT-FIG. 2. *Terrestrisuchus gracilis* gen. et sp. nov. A–C, cranium in left lateral view: A, reconstruction; B, structure of the preserved material; C, restoration of the articulations.

Ectopterygoid. Two of these bones have been identified and one, on P. 79/1a, is almost perfect. The ectopterygoid is triradiate and consists of a jugal process and lateral and medial palatal processes. The palatal processes both taper distally and diverge at about 80°. The lateral process overlapped the transverse process of the pterygoid ventrally. The lateral part of the medial process also articulated with the ventral surface of the pterygoid but its tip passed through a notch in that bone and then fitted against its dorsal surface. The jugal process, which curves antero-dorsally, is oval in cross-section where it joins the palatal processes. Laterally this process expands and divides to form a pair of articular surfaces for the jugal.

Palatine. The palatines are large bones that covered much of the ventral surface of the snout. Each articulated medially with the pterygoid and vomer and laterally with the maxilla. The lateral edge of the palatine was horizontally orientated and, as the medial edge lay dorsal to the lateral, the palate was vaulted. Four good



TEXT-FIG. 3. *Terrestrisuchus gracilis* gen. et sp. nov. A–C, cranium in ventral view: A, reconstruction; B, restoration of the articulations; C, structure of the preserved material.

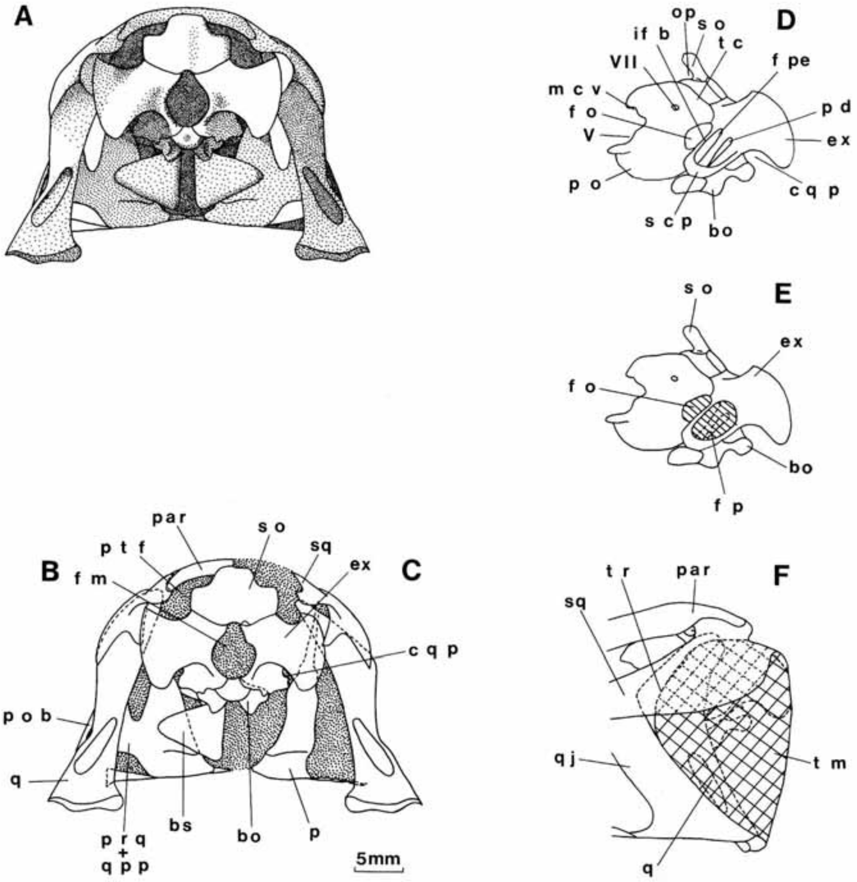
specimens of the palatine are preserved. This element is basically a flat plate of bone whose medial outline is convex anteriorly and slightly concave posteriorly. The lateral outline is straight centrally but notched anteriorly and posteriorly. The bone is thickened where it butt-jointed to the maxilla. No details of the articulations with the pterygoid are preserved. A facet for articulation with the vomer is present on the anterior margin of the ventral surface. The ventral surface of the palatine is smooth and approximately flat. Antero-laterally it bears a pair of hollows and an intervening ridge and in addition it was traversed by a step-like change in height that runs in a line directed postero-medially. These features imply that a soft palate may have extended over the palatines and that the functional choanae may have lain behind them.

Pterygoid. The pterygoid is well known from one almost complete specimen (P. 112/1) and others that are well preserved but incomplete (P. 78/1a and P. 47/22). The pterygoid is composed of three processes: palatal, transverse, and quadrate. The palatal process is a long, tapering plate of bone that extended anteriorly along the palate adjacent to its pair across the midline. The process is straight medially but did not suture to its counterpart and thus they were separated by a narrow interpterygoid vacuity. The lateral margin of the palatal process is also straight except for a small, tapering, antero-laterally directed palatine process. The tip of the palatine fitted into the notch that lies anterior to this process. The palatal process is strengthened medially by a low ridge. A deep, conical hollow is formed at the posterior end of the palatal process where it intersects with the transverse process. The posterior edge of the transverse process is concave whilst the lateral is slightly convex. The postero-lateral tip of this process was extended into a point. The anterior edge bears a notch for articulation with the ectopterygoid and longitudinal grooves mark the position of articulation of the lateral palatal process of that bone. The transverse process is twisted along its length so that its antero-lateral corner lies dorsal to its postero-lateral corner. The quadrate ramus of the pterygoid is approximately triangular in outline and its main surface faced postero-medially. The original outline of this process is uncertain and it is not known how it articulated with the pterygoid ramus of the quadrate. The posterior surface of the quadrate ramus is traversed by a ridge towards its ventral end and just dorsal to this the bone is deeply hollowed out. This hollow formed a cotyle for articulation with the basipterygoid process of the basisphenoid. This articulation was probably moveable. A small hook of bone, visible in palatal view, extends from the medial end of the ridge.

Vomer. No examples of this element are present but its outline can be reconstructed with fair certainty. The details of its structure are based on the vomer of *Sphenosuchus*.

Quadrate. There are seven quadrates preserved and, although none is perfect, in combination they give an almost complete picture of the structure of this bone except for some uncertainty as to the extent of the pterygoid process. The quadrate is a pillar-like bone that sloped strongly antero-dorsally. It consists of a triangular dorsal part with an approximately rectangular ventral extension that expands slightly towards its distal end. The bone is twisted centrally so that the external surface of the dorsal part faced laterally and very slightly posteriorly whilst the ventral part faced postero-dorsally and slightly laterally. The mandibular condyle faced postero-ventrally; this surface is expanded medially but narrows towards its lateral edge. A deep cavity or conch is present in the posterior surface of the bone in the same position as that of a lizard. The lateral edge of the ventral portion of the bone is broad and dorsally it merges with the lateral surface of the pterygoid ramus. The quadratojugal articulated with this edge of the bone. The dorsal edge of the quadrate is almost straight and sloped anteriorly, ventrally, and laterally. This edge is thin anteriorly but thickens posteriorly where it buttressed under the squamosal. The lateral surface of the dorsal part of the bone is smooth and slightly concave. A faint ridge runs along its dorsal margin diverging anteriorly from the dorsal edge. This ridge formed the antero-dorsal margin of the tympanic membrane. The pterygoid ramus is very thin and its outline is not fully known. As preserved, this projection has straight, parallel, dorsal, and ventral edges and its distal margin is slightly convex. The process was inclined ventrally and antero-medially.

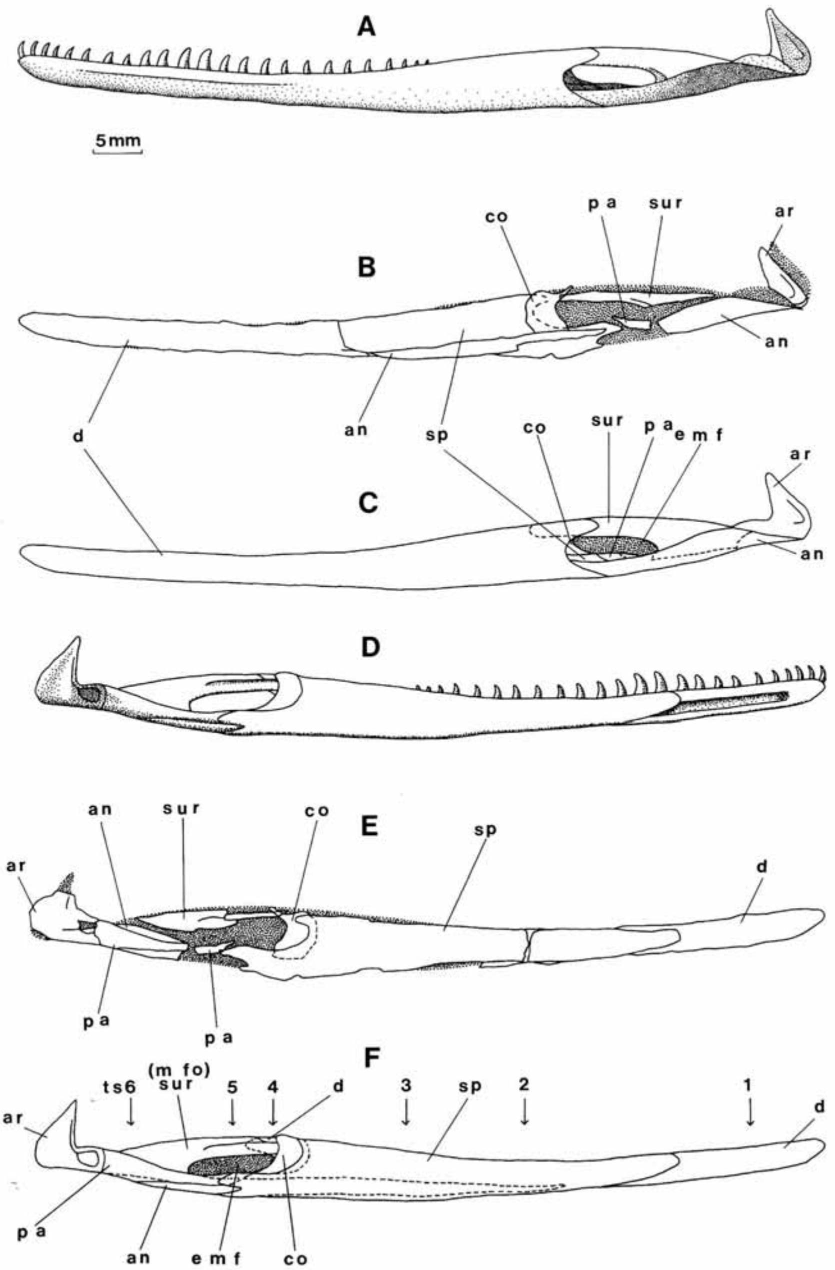
Basioccipital. The structure of this bone is well displayed by an articulated specimen on P. 78/1a, and a second, individual bone (P. 62/20) freed from most adhering matrix. The basioccipital consists of an approximately square body connected by a narrow neck to a swelling that formed the occipital condyle, the posterior end of which is depressed to form a small notochordal pit. The dorsal surface of the basioccipital formed the posterior part of the floor of the cranial cavity. This surface is smooth and slightly concave across its length. Flanking this surface are two articular facets: one for the exoccipital and a second, more anterior, facet for the basisphenoid. The anterior edge of the basioccipital also articulated with the basisphenoid. The basioccipital is hollow and this cavity opens into an approximately square foramen on the ventral surface of the bone. This basioccipital fossa is presumed to be part of the ramifications of the Eustachian tube system. Basioccipital tuberii are present posteriorly and the lateral surfaces of these projections are hollowed out into shallow cavities that faced posteriorly and slightly laterally. These cavities were for insertion of the subvertebral muscles.



TEXT-FIG. 4. *Terrestrisuchus gracilis* gen. et sp. nov. A–C, cranium in posterior view: A, reconstruction; B, restoration of the articulations; C, structure of the preserved material; D, reconstruction of the braincase; E, position of the fenestrae ovalis and pseudorotunda; F, reconstruction of the tympanum.

Basisphenoid. No element has been satisfactorily identified as a basisphenoid and thus this element has been reconstructed like that of *Sphenosuchus*.

Exoccipital. The exoccipitals can be completely described as six examples of this bone are preserved. The left exoccipital, comprising specimen P. 65/67, was used as the basis of this description as it is in excellent condition and is freed from nearly all adhering matrix. The 'exoccipital', as described, is composed of the fused exoccipital and opisthotic. The paraoccipital processes were swept backwards and expand dorso-ventrally towards their distal ends. The concave, thickened, dorsal edge of each process formed the ventral margin of the post-temporal fenestra. The distal end of the paraoccipital process articulated with the squamosal. The supraoccipital



TEXT-FIG. 5. *Terrestrisuchus gracilis* gen. et sp. nov. Left mandible in A–C, lateral, and D–F, medial views; A, D, reconstructions; B, E, structure of the preserved material; C, F, restorations of the articulations.

articulated with the dorsal margins of the anterior portions of the exoccipitals and also with flanges that they sent out above the foramen magnum. Anteriorly the exoccipital articulated with the prootic. A subcapsular process is present antero-ventrally and the lateral surface of this articulated with basisphenoid. The fenestra ovalis was formed at the junction with the prootic. Postero-ventral to this foramen is the foramen perilymphaticum separated from the ovalis by a narrow interfenestral bar. The perilymphatic duct opened posterior to the foramen perilymphaticum. This duct is confluent medially with the rest of the metotic fissure that served for the exit of nerves IX–XI.

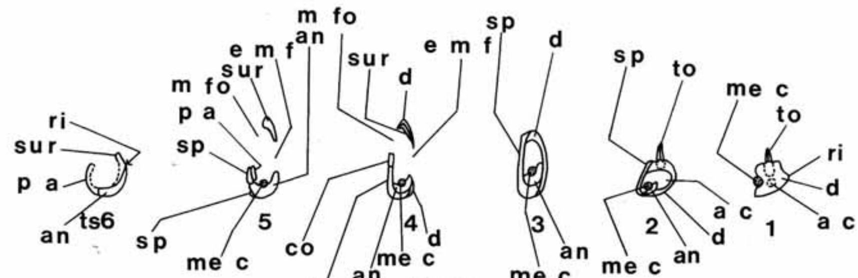
Laterosphenoid. No examples of the laterosphenoid have been identified but the structure of the prootics suggests their original presence. They were certainly present in *Sphenosuchus*.

Prootic. Only a single specimen of the prootic is preserved and unfortunately even this bone is in poor condition. It lies in lateral view, partially articulated with the exoccipital, on P. 47/22. The postero-dorsal edge of the prootic attached to the supraoccipital and the dorsal edge, which is straight and was horizontally orientated, articulated with the parietal. The prootic met the laterosphenoid anteriorly where it formed the posterior margin of the foramen ovale for the exit of the fifth cranial nerve. A notch, dorsal to the foramen ovale, could be part of a foramen for the middle cerebral vein. The ventral edge of the prootic articulated with the basisphenoid.

Supraoccipital. Two examples of this bone are preserved: one of these, on P. 47/22, is complete but has only its posterior and right aspects exposed whilst the second, P. 31/11, has been freed from matrix but is incomplete ventrally. The posterior part of the supraoccipital forms an occipital plate that sloped antero-dorsally at about 45°. The ventral edge of the bone articulated with the exoccipitals. The lateral margins of the occipital plate bear parallel-sided, roughened surfaces that, by analogy with the modern crocodile, were for the attachment of cartilages that partly filled the post-temporal fenestrae. The dorso-lateral edges of the plate are concave and formed parts of the margins of the post-temporal fenestrae. The dorsal edge of the occipital plate articulated with the ventral surface of the parietal by means of two oval articular facets. The posterior surface of the occipital plate is smooth and flat except for a low, centrally positioned, dorso-ventrally directed ridge. The supraoccipital sends projections anteriorly, from the lateral sides of the occipital plate, and these house segments of the osseus labyrinth.

Mandible. As reconstructed (text-figs. 5 and 6) the mandible is long and slim with a very long dentary and well-developed splenial. The angular is also large but, in contrast, the other bones are rather small. The articular is a fragile bone with medial and dorsal foramina. A dorsal process extends, from the articular, medial to the quadrate cotyle. The symphyseal area is small and the splenials do not reach the ends of the dentaries.

Angular. Five angulars are preserved and together they give a complete picture of the structure of this bone. The angular is long and slender and whilst it formed much of the lateral wall of the posterior end of the mandible it was only slightly exposed medially. The bone is rod-like anteriorly but posteriorly it is flattened; it tapers to a point anteriorly and posteriorly. The anterior portion of the bone is rounded off ventro-laterally and is hollowed



TEXT-FIG. 6. *Terrestrisuchus gracilis* gen. et sp. nov. Transverse sections of the left mandible, for positions of the sections see text-fig. 5F.

out medially forming the Meckelian canal. The anterior portion of the angular lay against the dentary and fitted into a groove in the splenial. More posteriorly the bone articulated dorsally with the surangular and medially with the prearticular. More posteriorly still it fitted against the articular.

Articular. Only two of these elements are preserved and both are on P. 78/1a in articulation with the other skull bones. The left of these is well preserved but has only its ventral surface exposed. The lateral, medial, and posterior aspects, and part of the dorsal surface, of the right are visible but the bone has been crushed latero-medially. The articular is a thin walled, hollow bone and foramina open into it on its dorsal and medial surfaces. The medial foramen is large and oval but only a portion of the dorsal opening is visible. The articular surface for the quadrate lay posterior to the medial foramen. The bone supporting the deep cotyle for the quadrate is thin and, unexpectedly, interrupted by the dorsal foramen. Posterior to the articulation for the quadrate the medial part of the articular is expanded dorsally into a tapering process. This element articulated laterally with the angular and anteriorly with the prearticular. Unlike this bone in the modern crocodile, the articular had, at the most, only a very small contact with the surangular.

Coronoid. A single, right coronoid is contained, in lateral view, on P. 63/8. This bone is in very poor condition and was only identified because of its association with a splenial. The specimen is crushed and, as preserved, its surface is slightly convex. The complete posterior edge is concave where this element would have bordered the mandibular fossa. Anteriorly the bone is convex where it fitted into the coronoid notch of the splenial. No articular facets for the splenial are preserved.

Dentary. This element is better represented than the other bones of the lower jaw as there are six examples preserved. The dentary is a long slender bone whose distal end curves slightly dorsally. Anteriorly the ramus of the dentary is parallel sided but posteriorly it increases in height. The lateral edge of the bone is smooth and, anteriorly, bears a low ridge that runs parallel to its dorsal margin. The medial surface is traversed by the Meckelian canal. This canal terminates in a small hollow anteriorly where it was joined to its pair on the opposing dentary. The area of the symphysis is smooth. The dentary articulated medially with the splenial and postero-ventrally with the angular. More posteriorly still it articulated with the surangular.

Dentary teeth. The alveoli of the dentary are positioned along its lateral side. When preserved the teeth are fairly even in their development although there is evidence of a slight increase in height centrally. The dentary has been restored with twenty-four teeth although this may be slightly more than were originally present. The posterior end of the dentary has been restored without any teeth. There is no direct evidence for this unusual condition and it is postulated because of the length of the mandible and the sizes of the other bones. The anterior dentary teeth bore anterior and posterior cristae; they were slim, pointed, and recurved. The roots were oval in cross-section. The more posterior teeth were laterally compressed although otherwise they were pointed, bore anterior and posterior cristae, and were recurved like the anterior teeth. They differ from the latter in bearing serrations on their posterior edges. These are only visible ventrally but it is probable that they extended all along the posterior cristae.

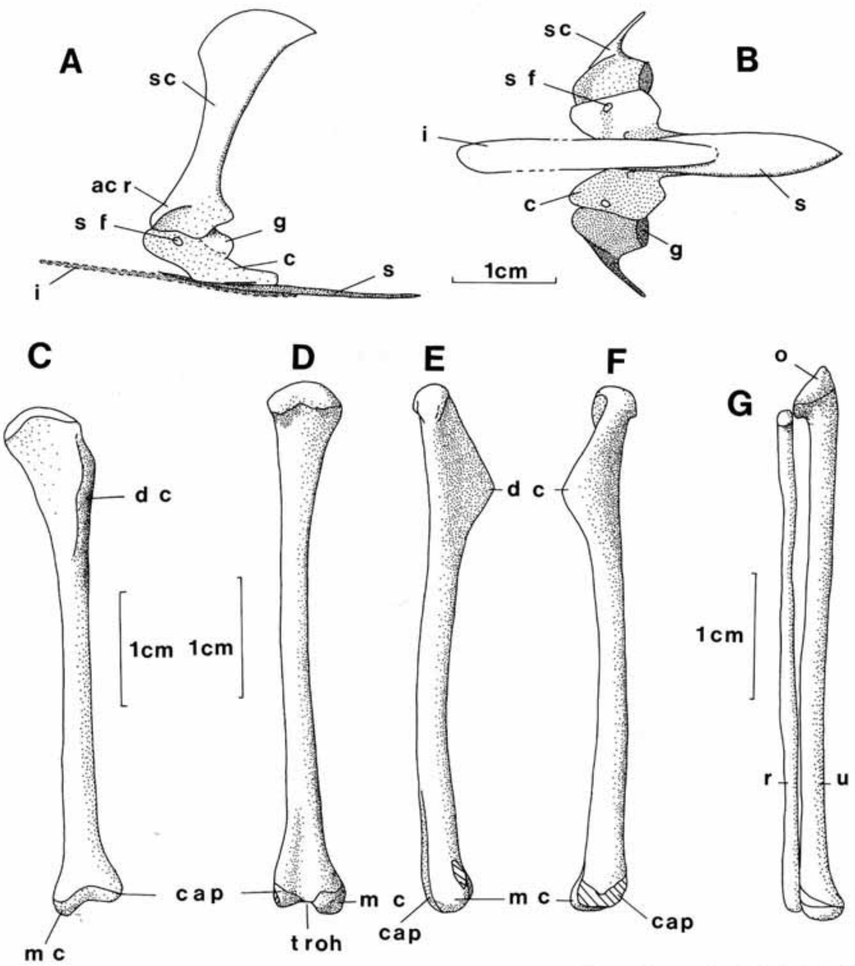
Prearticular. A single, right prearticular is preserved on P. 78/1a, and it is exposed in medial and lateral views. This bone expands posteriorly and whilst its ventral edge is almost straight its dorsal edge is slightly concave. The postero-medial surface is strongly convex but anteriorly the bone is flattened. Posteriorly it articulated with the articular and anteriorly it fitted lateral to the splenial. Postero-ventrally it fitted against the medial edge of the angular but more anteriorly it shifted its articulation on to the dorso-medial edge of that bone.

Splenial. Five splenials are preserved and the right on P. 63/8 is almost complete. The dorsal edge of this element is very slightly concave anteriorly and very slightly convex posteriorly. The posterior margin of the bone is incised by a large notch that articulated with the coronoid and a smaller, ventrally placed notch against which the angular fitted. The ventral edge of P. 63/8 is poorly preserved and has been reconstructed as slightly convex. The medial surface of the bone, as preserved, is flat. The ventro-lateral margin of the bone forms a groove which formed an articular surface for the angular.

Surangular. A single surangular is present on P. 78/1a and, unfortunately, this bone has been fractured centrally and its anterior end has been lost. The posterior part of the bone is approximately triangular and it has an antero-dorsal extension that runs above the external mandibular foramen. Anteriorly the dorsal edge of the bone projects medially so that it has an inverted V-shape in cross-section. This anterior process of the surangular fitted within the dentary. The lateral surface of the bone is convex across its longitudinal axis. Postero-ventrally a ridge is visible running parallel to the posterior part of the external mandibular foramen. Posteriorly this crest turns to run postero-dorsally and the angular buttressed under it. Below this ridge the ventro-lateral surface articulated with the medial surface of the angular.

DESCRIPTION: POSTCRANIAL SKELETON

Pectoral girdle. The material contains nine specimens of the scapula, eleven of the coracoid, three of the ossified sternum, but only one of the interclavicle. These allow a reconstruction of the pectoral girdle (text-fig. 7A, B) where only the shape of the interclavicle is in doubt. The scapula is waisted with a flattened dorsal portion drawn out into a point anteriorly and posteriorly. The convex dorsal edge of the blade is poorly finished and it is likely that it bore a cartilaginous suprascapula. The bone has an oval cross-section at its narrowest point and thickens ventrally. The ventral part of this element bears a distinct acromial ridge and its posterior edge is thickened to



TEXT-FIG. 7. *Terrestrisuchus gracilis* gen. et sp. nov. A–B, reconstruction of the pectoral girdle in left lateral and ventral views; C–F, left humerus, P. 47/22, in anterior, posterior, medial, and lateral views; G, left radius and ulna, P. 47/22, in lateral view.

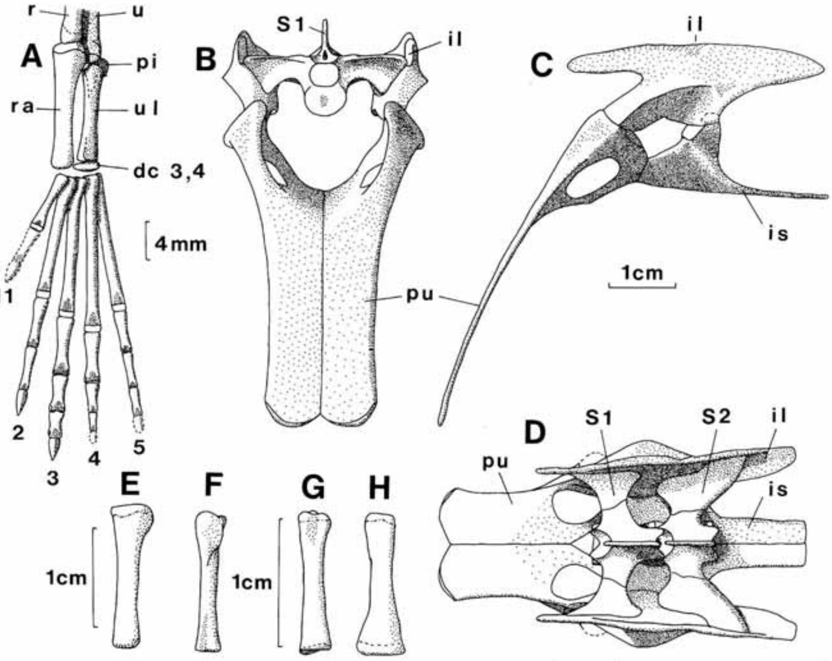
support the glenoid articular surface. This articulation is oval and slightly concave; it faced posteriorly, ventrally, and slightly medially. The medial surface of the ventral part of the bone lacks the process found in *Sphenosuchus*. The coracoid consists of a thickened central region supporting the glenoid articulation, and a much thinner anterior plate perforated by the supracoracoid foramen. The anterior plate is approximately triangular in outline. Posteriorly the bone is drawn out into a long tapering extension. The ventral surface of this process bears a deep trough bounded dorsally by a horizontally directed ridge. This ridge is homologous with the biceps tubercle in *Sphenosuchus* (Walker 1972). The edges of the sternum fitted into these troughs as shown by the articulated girdle of *Pseudohesperosuchus* (Bonaparte 1971*b*). The portion of the glenoid articular surface supplied by the coracoid is oval in outline and flat. This facet faced posteriorly, dorsally, and laterally. The coracoid is very similar to the problematical bone of *Hesperosuchus* (Colbert 1952). The preserved specimen of the interclavicle is very damaged and its original shape and length are uncertain. As preserved, this bone is elongated, flattened, and has parallel edges. The sternum is a thin, fragile bone. This ossification is smooth on both surfaces, its lateral edges are convex, and it is pointed anteriorly and posteriorly. The interclavicle fitted against its antero-ventral surface.

Humerus. There are sixteen humerii preserved and text-fig. 7 C–F shows the most complete of these which is only slightly damaged distally. The humerus is a long, slender bone that was held vertically (text-fig. 14). The head extends about a third of the way along the length of the bone and is set off at a small angle to the direction of the shaft. This means that the centre of the thickened, proximal, articular surface is slightly medial to the line of the shaft. The deltopectorial crest is well developed; its surface is convex laterally and concave medially. In lateral view the crest has a triangular outline and rises to a point just over half-way along its length. The central region of the shaft is thin walled and has a circular cross-section. The capitellum, or radial condyle, and medial convexity are well developed. They are separated by a groove or trochlea that articulated with the olecranon of the ulna. In life the distal articular surfaces faced downwards which implies that the forearm was held in an extended position.

Antebrachium. The ulna is a slender bone with a long shaft but only slight proximal and distal expansions (text-fig. 7G). The proximal part of the bone is formed into an olecranon. The head of the bone is approximately triangular in proximal view with a concave anterior edge that fitted against the flattened proximal end of the radius. The ulna has a double flexure giving it a very slight S-shape in lateral view. The shaft is circular in cross-section and thin walled. The distal end of this element is slightly expanded posteriorly giving it a tear-drop outline in distal view and its medial surface is flattened anteriorly where it fitted against the distal end of the radius. The distal articular surface is slightly concave. The radius is also a slender bone with poorly developed proximal and distal expansions. The proximal end is flattened antero-posteriorly, whilst the distal expansion is oval in distal view. The shaft of the radius is straight and parallel sided; it is hollow with a slightly oval cross-section.

Carpus and manus. The carpus is fully crocodilian and is composed of just four ossifications: the radiale, ulnare, pisiform, and the fused remains of distal carpals three and four (text-fig. 8A, E–H). In addition, although the proximal carpals are relatively longer, their articular surfaces can be homologized with those of the modern crocodile. Specimen P. 72/1 includes an almost perfect set of these bones comletely freed from matrix. Thus on the reconstruction only the details of the articulations and the terminal phalanges on digits one, four, and five are conjectural. The radiale is a slender bone with a slight distal expansion and a more pronounced proximal one where it contacted the radius and ulna. The articular surface for the radius is oval in shape whilst that for the ulna is triangular. The lateral surface of the distal portion of this bone bears a trough for muscular insertion. The ulnare is more expanded distally than proximally. The proximal articulation for the ulna is approximately triangular whilst the distal for the fused distal carpals is tear-drop shaped. The pisiform is an irregular pear-shaped bone. It is small relative to those of *Protosuchus* and the modern crocodiles suggesting that the wrist was less flexible in *Terrestrisuchus*. The bone representing the distal carpals is flattened and triangular in proximal view. The manus has been reconstructed as digitigrade. The preserved ungual phalanges are curved, pointed, and bear grooves on their lateral and medial surfaces. It would thus appear that digits two and three at least terminated in a claw.

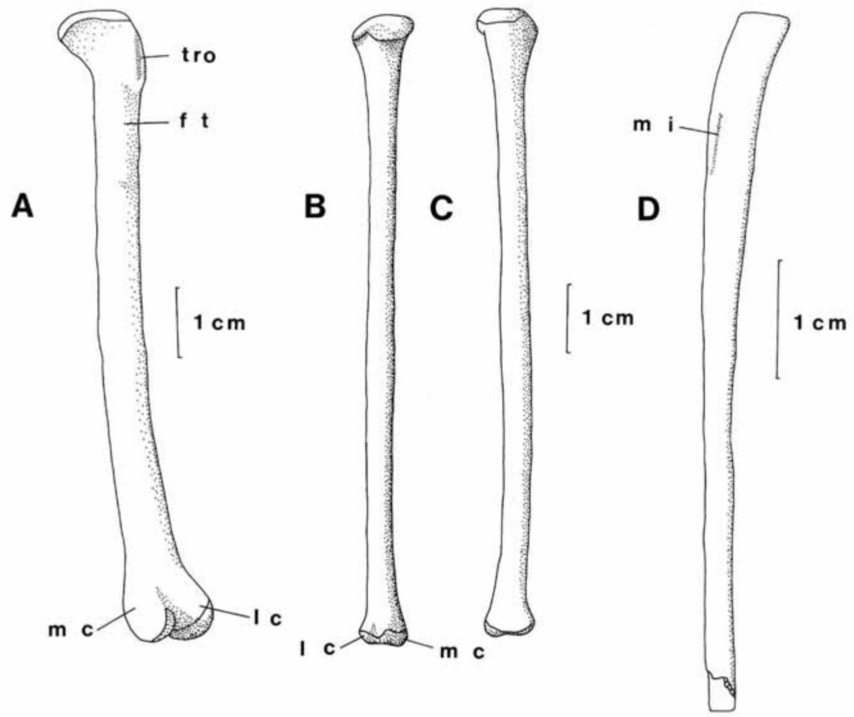
Pelvis. Eleven specimens of the ilium are preserved, sixteen of the pubis, and six of the ischium. The fine quality of these bones allows the pelvic girdle to be completely reconstructed (text-fig. 8B–D). The iliac blade, which is rather low, extends anteriorly into a long, laterally compressed process whilst the posterior projection is deeper anteriorly but tapers distally. Part of the rib of the first sacral vertebra attached to the ventral edge of the anterior projection whilst the rest attached to the base of the ilium (text-fig. 13A). The rib of the second sacral vertebra attached to the base of the ilium and also fitted around a strong ridge that runs along the ventral edge of the



TEXT-FIG. 8. *Terrestrisuchus gracilis* gen. et sp. nov. A, reconstruction of left carpus and manus in anterior view; B–D, reconstruction of pelvis, based on P. 72/1, in anterior, left lateral, and dorsal views (in B the second sacral vertebra and ischia are not included); E–F, left radiale, P. 72/1, in anterior and lateral views; G–H, left ulnare, P. 72/1, in posterior and lateral views.

medial surface of the posterior projection. The ventral edge of the ilium is notched where it bordered the acetabular foramen. The bone forming the medial wall of the acetabulum is thin and the supra-acetabular ridge is strongly developed. The ilium is thickened where it supports the articulations for the pubis and ischium. The pubes are well developed and their anterior ramii were joined medially although it seems likely that there was a break in the symphysis below the acetabulum. Each pubis bears a well-developed, oval, obturator foramen. The ischia bore flattened posterior projections that joined along the midline. The dorsal part of the ischium is thickened where it buttressed against the ilium. The anterior edge is thin and straight for articulation with the pubis. The antero-dorsal margin of the ischium is rounded off where it bordered the acetabular foramen.

Femur, tibia, and fibula. Although fourteen specimens of the femur are preserved, none is quite perfect. Text-fig. 9A shows the best example which is on block P.24/39a. The femur is a slender bone with a slightly developed head which is flattened and twisted on the shaft such that it was directed antero-medially. In this position it would have buttressed under the supra-acetabular ridge of the ilium if the femur were, as reconstructed, held vertically. There is no greater or lesser trochanter but the proximal part of the shaft bears a weakly developed fourth trochanter. The proximal end of the femur bears another trochanter which takes the form of a low ridge running along the posterior margin of the head. The shaft has a slight sigmoid flexure that is much less apparent than in the modern animal. The medial and lateral condyles are well developed for articulation with the tibia. The fibula articulated with a facet on the lateral edge of the lateral condyle. The tibia is a slender bone (text-fig. 9B, C) that was slightly longer than the femur. There is no complete fibula present and the illustrated specimen, P. 130/1

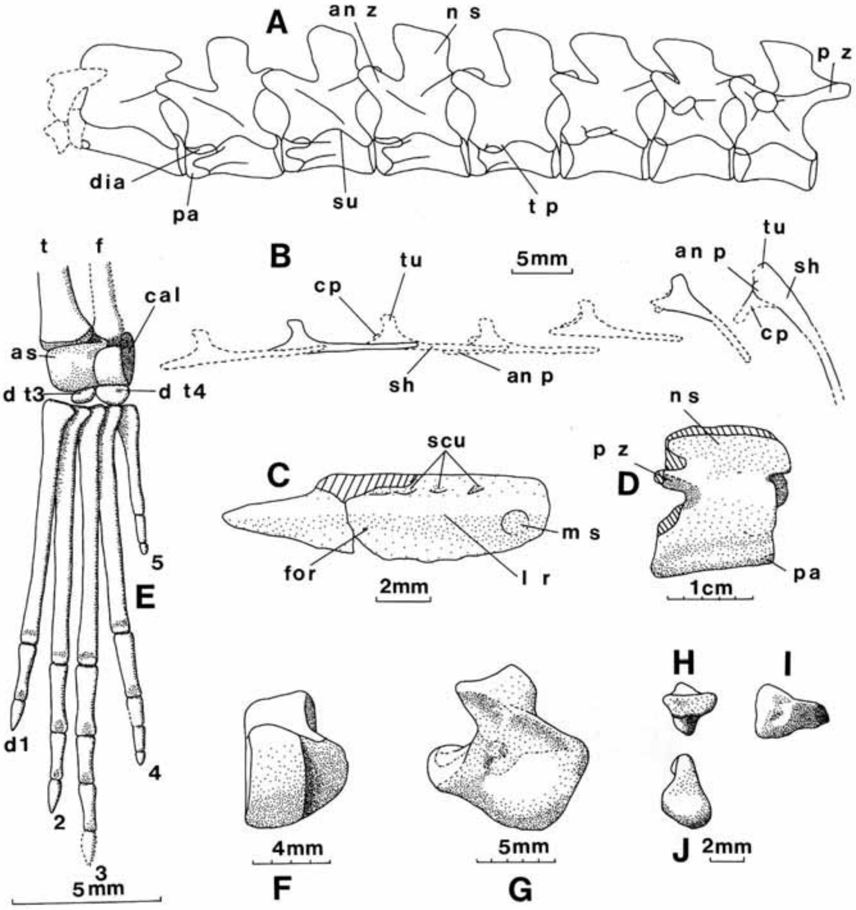


TEXT-FIG. 9. *Terrestrisuchus gracilis* gen. et sp. nov. A, restoration of right femur, based on P. 24/39a, in postero-medial view; B–C, left tibia, P. 11/1, in posterior and anterior views; D, left fibula, P. 130/1, in lateral view.

(text-fig. 9D), is incomplete distally. This element is a slender bone that is flattened proximally and bears a slight crest, for muscle insertion, on the lateral surface of its anterior edge. The distal expansion of the bone is slight.

Tarsus and pes. There are just four bones in the tarsus: the astragalus, calcaneum, and distal tarsals three and four (text-fig. 10E–J). The proximal tarsals articulated together by a ball and socket joint, with the astragalus functionally part of the crus whilst the pes, distal tarsals, and calcaneum moved as a unit on the astragalus and fibula. The calcaneum bears a well-developed tuber. The reconstruction of the tarsus is based on specimen P. 47/21a which comprises a virtually perfect set of tarsals completely freed from matrix. The medial surface of the calcaneum bears a circular socket, which accepted the peg of the astragalus, and a projecting lip of bone that lay posterior to the peg. Distal tarsal three, as preserved, is approximately cylindrical in shape. Distal tarsal four is larger than the other distal tarsal and consists of two expansions set at right angles to each other. The anterior of these lay horizontally whilst the posterior lay vertically and both were triangular in outline. The first four metatarsals are long and were approximately equal in length whilst the fifth is reduced. The fifth is primitive for a crocodile in that it is still about half the length of metatarsal four and bears two phalanges although these have been reduced to two small nubbins of bone. The proximal expansion of metatarsal five is bulbous and it bears a flange that fitted behind the proximal expansion of metatarsal four. The phalangeal formula is 2, 3, 4, 4, 2.

Armour and gastralia. A single row of scutes was present on each side of the dorsal midline but there is no evidence of any ventral or dorsal paramedial scutes. The armour is not shown in the reconstruction. The thoracic

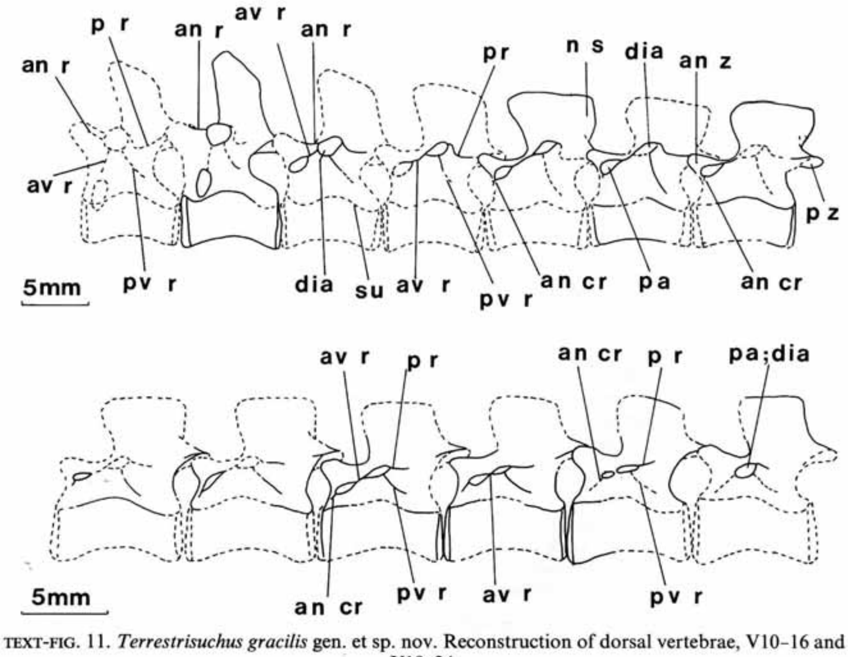


TEXT-FIG. 10. *Terrestrisuchus gracilis gen. et sp. nov.* A, reconstruction of cervical vertebrae, based on P. 79/1; B, reconstruction of cervical ribs; C, left scute, P. 123/1, in dorsal view; D, axis, P. 47/22a, in right lateral view; E, reconstruction of left tarsus and pes in anterior view; F, right calcaneum, P. 73/1, in anterior view; G, right astragalus, P. 110/1, in anterior view; H–J, right distal tarsal four, P. 47/21a, in anterior, dorsal, and lateral views.

scutes are basically leaf-shaped (text-fig. 10C) with an anterior peg that fitted into a triangular groove on the ventral surface of the adjacent plate. Each scute bears a prominent ridge along its midline and is sculptured medial to this ridge. A muscle scar is present postero-laterally. The gastralia, which are single ossifications, are broad, flattened, and V-shaped. The lateral projections of these elements curved slightly dorsally.

Atlas–axis complex. The atlas intercentrum, pro-atlas, and axis rib are not present in the material and the other atlantal elements are poorly preserved. The axis is in good condition on F. 47/22a (text-fig. 10D). The remains of the atlas neural arch show that it consisted of a dorsal flange that lay nearly horizontally and protected the dorsal part of the spinal cord, and a cresentric ventral part that articulated with the atlas intercentrum, the basioccipital condyle, the odontoid, and the axis centrum. The atlas rib was a cylindrical rod of bone. Only a damaged nodule of bone is preserved representing the odontoid which was sutured, not fused, to the axis centrum. The figured specimen of the axis lacks an anterior zygapophysis. Specimen P. 78/1a shows this to have been an oval facet that faced dorso-laterally. There is only a single articular surface for the axis rib.

Cervical vertebrae and ribs. The cervical vertebrae have been reconstructed (text-fig. 10A) on the basis of an articulated, although damaged, cervical series on P. 78/1 and individual examples of V2–6, V8, and V9 which are well preserved on P. 79/1. The only doubtful parts of this restoration are the exact shapes of the neural spines which show some variation. A slight hypapophysis is present on V3 but such a flange is not found on the axis or on any of the more posterior vertebrae. The parapophyses on V3 and V4 are approximately oval in outline whilst more posteriorly they become triangular. On Vertebrae V3–5 the articular surface of the parapophysis merges with that of the diapophysis but posteriorly they are distinct. On the anterior vertebrae the parapophysis is supported by a strong ridge but this has faded out by V7. The structure of the transverse process, bearing the diapophysis, changes markedly along the sequence V3–9. On V3 the transverse process is just a slight protuberance with a ridge running back from it but the diapophysis moves progressively postero-dorsally along the series V3–9 and the transverse process increases in length. On V6 and V7 the transverse process is dorso-ventrally flattened and bears two ridges running along its anterior and posterior margins. On V8 a third ridge is developed postero-ventrally and on V9 a fourth antero-ventral ridge is present. The neural spines are flattened without trace of any dorsal thickening. A deep pit is present at the base of the posterior edge of the neural spine whilst a shallower one is present below its anterior edge. The anterior and posterior zygapophyses are well developed. The suture between the neural arch and centrum runs through the transverse processes on V3–5 and just below it on V7.

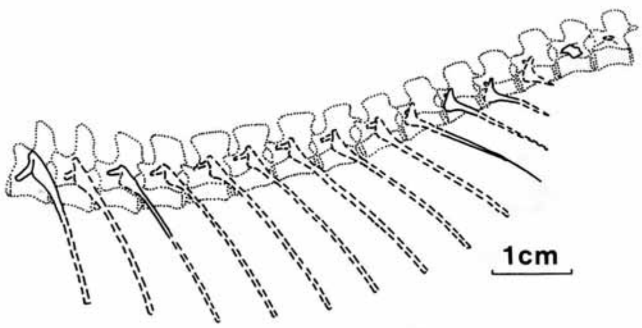


TEXT-FIG. 11. *Terrestrisuchus gracilis* gen. et sp. nov. Reconstruction of dorsal vertebrae, V10–16 and V19–24.

The cervical ribs are generally poorly preserved but P. 79/1a bears a well-preserved rib of V4 and P. 78/1b shows the structure of those of V8 and V9. It is thus possible to reconstruct the cervical ribs with confidence (text-fig. 10). The ribs of V3 to V7 are all similar and each extends anteriorly into a pointed, tapering process and posteriorly into a shaft that projected parallel to the vertebral column. The tuberculum and capitulum diverge at about 45° to one another. The rib of V8 possesses a pointed anterior process but the shaft is now longer and extends ventro-laterally. The anterior projection of V9 has been converted into a thin, rounded flange and the shaft now extends to curve around the body. There is no evidence for the presence of a cartilaginous uncinate process on any of the ribs.

Dorsal vertebrae and ribs. Specimen P. 78/1b bears V10–18 in association but these vertebrae are not well preserved. Block P. 72/1 contains the last seven presacrals, in better condition, in articulation with the two sacrals. There are some fine examples of individual vertebrae (P. 30/1, P. 80/1) and the dorsal column can be reconstructed (text-fig. 11) although not with quite the same confidence as the cervicals. The number of presacral vertebrae has been taken as twenty-four as this is the number present in *Protosuchus* and *Orthosuchus*. The material of *Terrestrisuchus* only allows a minimum number of twenty-three to be established. There is no distinction between thoracic and lumbar subregions as even the final presacral vertebra bears a free rib. The structure of the centrum is basically unchanging along the dorsal series except that it becomes relatively longer posteriorly. The articular surfaces of the centra are platycoelous but the anterior is more deeply hollowed out than the posterior. The parapophysis moves dorsally within this vertebral series and by V12 has migrated to just antero-ventral to the transverse process. At the posterior end of this series it moves closer to the diapophysis and finally merges with it on V24. Posterior to V13 this articulation is supported by a crest anteriorly. Unlike the situation in the modern crocodile the parapophyses are never borne on the transverse processes. The ridges supporting the transverse process are the same on V10 and V11 as those on V9, however by V13 the anterior ridge has disappeared and the antero-ventral ridge joins to the parapophysis. The three remaining ridges are present all the way back to V23. The structure of the neural spines is well preserved on V14 and V16, on P. 78/1b, and there is no trace of any dorsal thickening. The zygapophyses of V10 and V11 are like those of the cervical vertebrae but by V15 they have come to lie more horizontally. Pits were present at the bases of the neural spines of all the dorsal vertebrae.

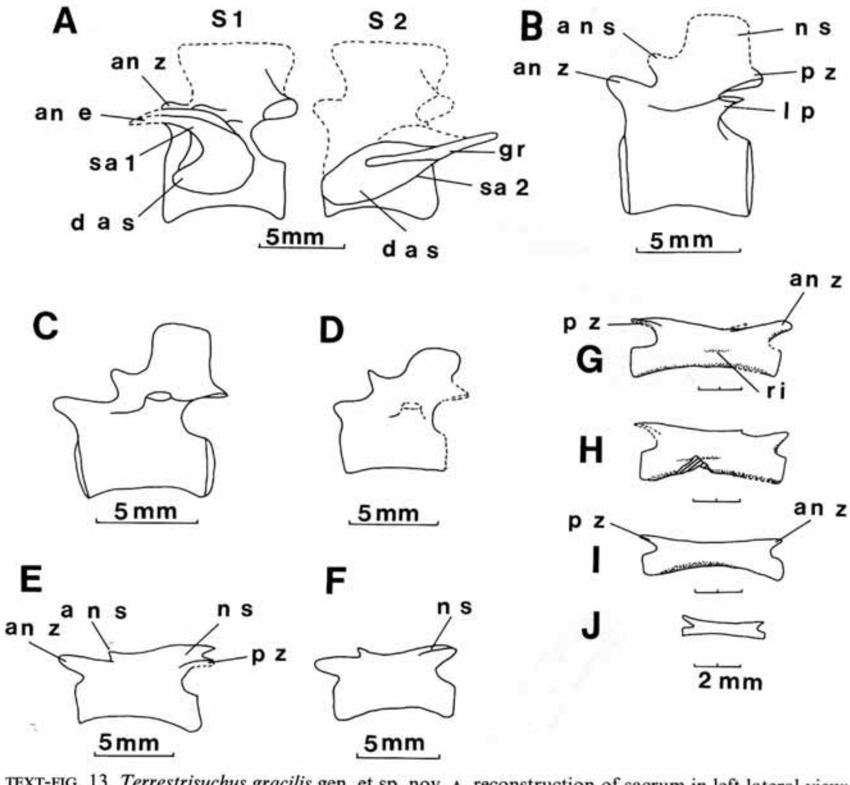
A fairly large number of dorsal ribs are preserved but few are in good condition. Text-fig. 12 shows what is believed to be an accurate restoration of these bones. The only significant reconstruction has been in the lengths of their shafts. All the ribs are dichocepalous except for that of V24 which is holocephalous. Rib ten on P. 78/1a is well preserved. The tuberculum is broad and flattened whilst the capitulum is circular in cross-section. The anteriorly projecting flange lies at about 45° to the plane of the articular processes. Rib sixteen, on the same specimen, is in fine condition. The tuberculum has now become just a small projection but the capitulum is well developed. The anterior flange is now triangular in outline and lies in the same plane as the heads of the bone. The ribs reduce posteriorly until that of V23 is just a flattened piece of bone with no shaft and barely distinguisable articular facets. The rib of V24 is exceptional in that it extended horizontally; it is flattened and has an approximately rectangular outline.



TEXT-FIG. 12. *Terrestrisuchus gracilis* gen. et sp. nov. Reconstruction of dorsal ribs, V10–24.

Sacral vertebrae. The first sacral vertebra is represented by four specimens one of which, P. 1/1, has been completely freed from matrix and is in excellent condition. The second sacral vertebra is less well represented in the material, but there is a fine specimen showing the centrum and rib in ventral view (P. 24/39e). The reconstruction of the sacrum on text-figs. 8B, D and 13A is thus considered to be accurate. The ribs of the first sacral vertebra are short and stout and they attach to transverse processes that arise from the complete dorso-ventral extent of the pedicels. Their distal articular surfaces for the ilia consist of a large ventral portion that faced ventrally, laterally, and slightly posteriorly, and a long tapering anterior extension. The transverse processes of the second sacral vertebra also originate from the whole height of the pedicels. The distal articular surfaces of these ribs are expanded anteriorly but taper posteriorly. Each articular surface bears a deep groove for articulation with the ilium.

Caudal vertebrae. The tail of *Terrestrisuchus* was very long and the number of caudal vertebrae has been estimated at about seventy. The tail can be split into two regions, 1 and 2, on the basis of the presence or absence of lateral processes (text-fig. 13B–J). These processes consist of ribs sutured to transverse processes. The proximal vertebrae of region 1 have short, stout centra and the main part of the neural spine is short and square. There is a small antero-dorsally directed accessory spine developed at the base of the anterior edge of the main neural spine.

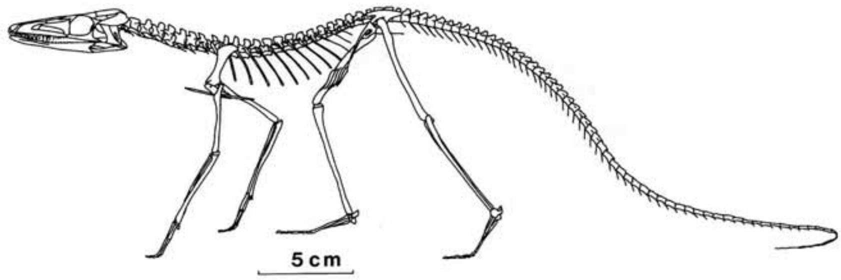


TEXT-FIG. 13. *Terrestrisuchus gracilis* gen. et sp. nov. A, reconstruction of sacrum in left lateral view; B–F, reconstruction of caudal vertebrae, in left lateral view, proximal region 1, medial region 1, distal region 1, proximal region 2, and medial region 2; G–J, distal region 2, P. 47/21, in right lateral view.

The lateral processes of these vertebrae exceed the length of the centrum and are swept back posteriorly and slightly dorsally. The centra of the vertebrae of the medial part of region 1 are more laterally compressed than those of the proximal region. The lateral processes project more directly laterally and are shorter than those on more anterior vertebrae. The distal vertebrae of region 1 show some change in the shape of the neural spine which now slopes posteriorly but the accessory spine is still present. The centrum is now more laterally compressed than those of the medial vertebrae and is relatively shorter. The lateral processes are further shortened. The more posterior of these vertebrae bear a small boss placed centrally on the lateral surface of the centrum. The proximal vertebrae of region 2 have centra that are relatively longer than those of the anterior vertebrae. There is still an accessory spine but the main neural spine is now very low and extended into a point posteriorly. The only difference in the medial vertebrae of this region is that the neural spine is rounded off posteriorly. More distally the bones become relatively longer and first lose all trace of neural spines and then zygapophyses.

Haemal arches. The extent of the haemal arches is uncertain although it is known that they were present anteriorly but did not continue to the end of the tail. They are basically rods of bone with a dorsal expansion that is pierced by a foramen. This expansion becomes relatively smaller towards the distal end of the tail. There is no evidence for the regional differentiation found in the chevrons of the modern crocodile.

Reconstruction and size. As restored *Terrestrisuchus* has a short trunk, long upright limbs, and a very long tail (text-fig. 14). The pelvis was held high above the pectoral girdle and both the manus and pes were digitigrade. The total length has been estimated to lie between 490 and 770 mm. It is not possible to be certain but it seems most likely that this material represents a small species rather than a collection of juveniles.



TEXT-FIG. 14. *Terrestrisuchus gracilis* gen. et sp. nov. Reconstruction based upon P. 47/21, 22.

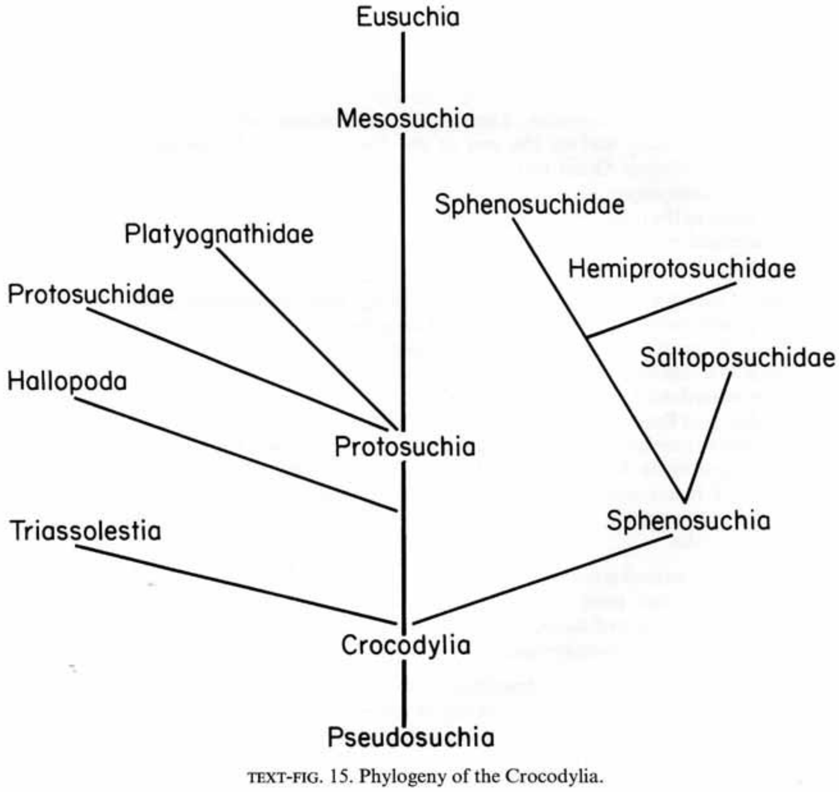
DISCUSSION

Crocodilian affinities. *Terrestrisuchus* is considered to be a crocodile because of the presence of an elongated radiale and ulnare, whose structure can be homologized with those bones of the modern crocodile. Other apomorphic characters for the order Crocodylia, present in this genus, are the absence of a descending process from squamosal to quadratojugal and the presence of a parallel-sided quadratojugal. (The quadratojugal of *Pseudohesperosuchus* is assumed to be specialized.) *Terrestrisuchus* has other character states considered by Langston (1973) and Nash (1975) to be diagnostic of the Crocodylia: external nares terminal in position; some development of a secondary palate; choanae posterior to the external nares; quadrate inclined and bordered by a long slender quadratojugal; pterygoids wide with deep wings; advanced crurotarsal joint; femur without a marked fourth trochanter and no development of a greater trochanter; external surfaces of the dorsal scutes sculptured.

A proposed classification of the crocodiles:

Order Crocodylia Gmelin 1788
  Suborder Triassolestia nov.
    Family Triassolestidae Bonaparte 1970
      Genus *Triassolestes* Reig 1963
  Suborder Sphenosuchia nom transl., ex. infraorder Sphenosuchia, Bonaparte 1971 *incertae sedis*: *Dibothrosuchus* Simmons 1965
    Family Saltoposuchidae nov.
      Genera *Saltoposuchus* Huene 1921, *Terrestrisuchus* gen. et sp. nov.
    Family Hemiprotosuchidae nov.
      Genus *Hemiprotosuchus* Bonaparte 1969
    Family Sphenosuchidae Huene 1922
      Genera *Pseudohesperosuchus* Bonaparte 1969, *Sphenosuchus* Haughton 1915, *Hesperosuchus* Colbert 1952
  Suborder Protosuchia Mook 1934
    Family Protosuchidae Brown 1933
      Genera *Erythrochampsa* Haughton 1924, *Notochampsa* Broom 1904, *Pedeticosaurus* Van Hoepen 1915, *Protosuchus* Brown 1933, *Orthosuchus* Nash 1968, *Stegomosuchus* Huene 1922, *Eupneumatosuchus* Crompton and Smith 1980
    Family Platyognathidae Simmons 1965
      Genus *Platyognathus* Young 1944
  Suborder Hallopoda Marsh 1881
    Family Hallopodidae Marsh 1881
      Genus *Hallopus* Marsh 1877
  Suborder Mesosuchia Huxley 1875
  Suborder Eusuchia Huxley 1875

The order Crocodylia is conventionally split into three suborders: Eusuchia, Mesosuchia, and Protosuchia. These are retained but an additional suborder is proposed, Triassolestia, for *Triassolestes*. This, the suborder Hallopoda, for *Hallopus*, and the suborder Sphenosuchia are all included in the Crocodylia. The suborder Triassolestia contains only *Triassolestes* in its own family, Triassolestidae. *Triassolestes* (Reig 1963; Bonaparte 1971*a*) is very tentatively included in the Crocodylia because of the presence of elongated carpals but otherwise it differs from the other crocodiles in having a coracoid without a dorso-ventral or postero-ventral projection and a non-crocodilian tarsus. In addition to these primitive characters it has some specialized features in that it has a reduced metatarsal one and the pes is functionally tridactyle. The suborder Sphenosuchia has been divided into three families: Saltoposuchidae, Hemiprotosuchidae, and Sphenosuchidae. These are linked by the presence of: a caracoid with a postero-ventral projection, a quadrate conch, and an ossified sternum (this character state is paralleled in *Hallopus*). The Hemiprotosuchidae and Sphenosuchidae, although distinct, are more closely related to each other than either is to the Saltoposuchidae. They are linked by the following character states: interpterygoid vacuities closed; frontals entering the supratemporal fenestrae; fused parietals; and scutes square or rectangular. All of these character states were developed in parallel in the Protosuchia. *Terrestrisuchus* and *Saltoposuchus* are classified together on the basis of the presence of a kidney-shaped squamosal. Additionally, a comparison of the skull, mandibular, and postcranial remains reveals many similarities in detail and argues strongly for their close relationship. The animals do differ in certain skull features sufficiently to separate them generically. For instance, the maxilla of *Saltoposuchus* lacks the fossa found in this bone of *Terrestrisuchus*. The Hemiprotosuchidae is a monotypic family specialized in that the supraorbital is incorporated into the skull roof (Bonaparte 1969, 1971). The members of the Sphenosuchidae are linked by the possession of: a reduced squamosal overlapped postero-laterally by the opisthotic, a longitudinal crest on the parietals, and a depression on the frontals (the latter two character states have been independently developed in the Protosuchia). The suborder Protosuchia is split into two families: the Protosuchidae with seven members and the Platyognathidae that contains only *Platyognathus*. The Protosuchia are a group that have many apomorphic characters: two supraorbital elements; absence of an obturator foramen in the pubis; entry of the frontals into the supratemporal fenestrae; midline fusion of the parietals (the last two character states are variable in this suborder and are also found in the Sphenosuchia); dorso-ventrally expanded coracoid and ischium; rod-shaped pubis partly or fully excluded from the acetabulum; the absence of an obturator foramen in the pubis; dorsal ribs flanged anteriorly and posteriorly; metatarsal five without phalanges; ventral scutes present (this character is variable); immovable basipterygoid articulations; quadrate and pterygoid fused to the braincase; straight groove on squamosal for ear flap; rectangular squamosals; square or rectangular scutes; and loss of interpterygoid vacuities (the last two character states were developed in parallel in the Sphenosuchia). The members of the Protosuchidae are united by having conical teeth that are unserrated. The posterior teeth of *Eupneumatosuchus* are flattened, however. The teeth of the South American sphenosuchid genera also lack serrations. The new material, recently described by Crompton and Smith (1980), of *Protosuchus* and *Eopneumatosuchus* has helped to confirm the close relationships of the Protosuchidae. *Eopneumatosuchus* itself clearly belongs in the suborder Protosuchia. *Platyognathus* (Young 1944; Simmons 1965) has a number of specializations which indicate that



TEXT-FIG. 15. Phylogeny of the Crocodylia.

it belongs in a family of its own: fused mandibular ramii (*Sphenosuchus* has developed this character state in parallel); procoelous vertebrae; teeth with a polygonal transverse section; terminal and confluent external naries; and anterior mandibular teeth projecting forward (this character state may also be present in *Notochampsa*). Although the classification presented here postulates much parallel evolution in the early crocodiles it is believed to have reduced it to a minimum. It is recognized that with better information on the less well-known genera the classification would probably alter.

Interrelationships of the suborders. There appears to have been a radiation of the Crocodylia represented by the Protosuchia, Triassolestia, and Sphenosuchia at the end of the Triassic (text-fig. 15). The upper Jurassic Hallopoda may have had a common ancestry with the Protosuchia as although *Hallopus* is specialized (Walker 1970, 1972) in having a functionally tridactyle pes, and a posteriorly rotated pubis has three characters otherwise only found in the Protosuchia—a dorso-ventrally expanded ischium and a rod-shaped pubis that is fully excluded from the acetabulum. These suborders, the Sphenosuchia and the Triassolestia, are proposed to have had a common pseudosuchian origin. The Sphenosuchia cannot be ancestral to the Protosuchia, as has often been thought, because of the presence of the quadrate conch and the structure of the coracoid. It is not considered possible to derive the coracoid of *Protosuchus* from those of the sphenosuchids. Furthermore, the secondary palate of the latter, as evidenced by those of *Terrestrisuchus* and *Sphenosuchus*, are not homologous with that of *Orthosuchus* but are convergent with the type found in birds (Walker 1972). *Sphenosuchus* itself is further removed from a protosuchian ancestry by its functionally tridactyle pes. The supraorbital of *Hemiprotosuchus* bars it from a protosuchian ancestry. The specialized structure of *Triassolestes* means that the Triassolestia cannot be the ancestral group of the protosuchids. The terrestrial, cursorial, quadrupedal crocodiles represented by the Hallopoda, Sphenosuchia, and Triassolestia have no known descendants and seem to have been a relatively short-lived phenomenon. These forms are diverse when they first appear at the Triassic–Jurassic boundary and by the end of the Jurassic are only represented by one highly specialized genus, *Hallopus*. Other terrestrial crocodiles evolved within the Mesosuchia but they never attained the same degree of cursorial adaptation. The early forms may have been outcompeted by the coelurosaurs as the latter became more highly adapted for a bipedal, cursorial mode of life. The Protosuchia diverged ecologically from the Sphenosuchia and adopted a way of life similar to that of the modern crocodiles.

Origin of the Crocodylia. The thecodonts have long been considered ancestral to the later archosaurian groups including the crocodiles and thus membership of this order was investigated in the light of knowledge of the structure of *Terrestrisuchus*, in an attempt to trace the early crocodilian suborders back to a common ancestor. The thecodonts were reviewed by Romer (1972) who divided them into four suborders. The first suborder Proterosuchia contains three families Proterosuchidae, Erythrosuchidae, and Prestosuchidae which are primitive groups showing no crocodilian affinities. The fourth family Proterochampsidae has specializations excluding it from a crocodilian ancestry as do the next two suborders Aetosauria and Phytosauria. The final suborder Pseudosuchia contains a wide variety of forms some of which have been classified here as crocodiles. Some of the pseudosuchids are specialized, and some are primitive, but no species gives any indication of the origin of the crocodiles.

Dibothrosuchus. This animal is poorly preserved and consists only of cranial fragments, a number of articulated vertebrae, and parts of a forelimb. Simmons (1965) considered it to be similar to *Hesperosuchus* which suggested a crocodilian affinity. It is tentatively included in the Sphenosuchia because of the presence of a postero-ventral projection on the coracoid.

Saltoposuchus. This genus was first described by Huene (1921) who divided it into two species *Saltoposuchus connectens* and *S. longipes*. Study of the material reveals that the remains are of four individuals of only one species. Within those numbered 12596 and 12597 the individual called *S. longipes* is simply a larger specimen of *S. connectens*. Furthermore, the material attributed to *Procompsognathus*, on find number 12597, is also of *Saltoposuchus*. In these remains there was an angular, identified by von Huene as a clavicle of *S. connectens*, from find 12597 which did not form part of the other two individuals. There are therefore the remains of three animals, all of the species *S. connectens*, on the two numbered finds from Heugelschen. The individual identified as *S. longipes* from Burreschen is also *S. connectens*. Knowledge of the material of *Terrestrisuchus* has made possible some reinterpretations of the material of *Saltoposuchus*. In find 12596 Huene's pterygoid is a left squamosal in dorsal view, his palatine a left quadrate in antero-lateral view, and his metatarsal an ulna. In find 12597 Huene's humerus fragment is a left frontal; his clavicle is a left angular in medial view; the pterygoids are squamosals in ventral view; the prefrontal is a left jugal in lateral view; the quadratojugal is a left quadrate and the right quadrate is a left quadrate. Walker (1968, 1970) was correct in assigning this genus to the Crocodylia. He correctly reidentified the 'lacrymal' as a jugal, but was mistaken in suggesting that the ischium was a coracoid. He suggested that the pubes belong to *Procompsognathus* but this is not the case.

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Explanation of abbreviations used in text-figs.

a n s	accessory neural spine
ac r	acromial ridge
a c	alveolar canal
an	angular
an cr	anterior crest
an e	anterior extension
an r	anterior ridge
av r	antero-ventral ridge
a f	antorbital fenestra
a p f	anterior palatal foramen
an p	anterior process
an z	anterior zygapophysis
ar	articular
as	astragalus
bo	basioccipital
bs	basisphenoid
cal	calcaneum
cap	capitellum
cp	capitulum
c	coracoid
co	coronoid
c q p	cranio-quadrate passage
d c	deltopectoral crest
d	dentary
dia	diapophysis
d 1–5	digits one to five
d a s	distal articular surface
dc 3, 4	distal carpals three and four
d t 3, 4	distal tarsals three and four
e	ectopterygoid
ex	exoccipital
e m f	external mandibular foramen
e n	external naries
f o	fenestra ovalis
f p	fenestra pseudorotunda
f	fibula
for	foramen
f m	foramen magnum
f pe	foramen perilymphaticum
f t	fourth trochanter
fr	frontal
g	glenoid
gr	groove
il	ilium
i t f	infratemporal fenestra
i	interclavicle
if b	interfenestral bar
i n	internal naries
i v	interpterygoid vacuity
is	ischium
j	jugal
l	lacrimal
l c	lateral convexity
l p	lateral process
l r	longitudinal ridge
m fo	mandibular fossa
m	maxilla
m f	maxillary fossa
me c	Meckelian cartilage
m c v	middle cerebral vein
m c	medial convexity
m i	muscle insertion
m s	muscle scar
n	nasal
n s	neural spine
o	olecranon
op	opening into cranial cavity
or	orbit
p v	palatal vacuity
pal	palatine
pa	parapophysis
par	parietal
p d	perilymphatic duct
pi	pisiform
p r	posterior ridge
p z	posterior zygapophysis
pv r	postero-ventral ridge
po	postorbital
p o b	postorbital bar
p t f	post-temporal fenestra
p a	prearticular
p f	prefrontal
p m	premaxilla
p o	prootic
p	pterygoid
p r q	pterygoid ramus of the quadrate
pu	pubis
q	quadrate
q p p	quadrate process of the pterygoid
qj	quadratojugal
ra	radiale
r	radius
ri	ridge
S 1, 2	sacral vertebrae one and two
sa 1, 2	sacral ribs one and two
sc	scapula
scu	sculpturing

sh	shaft	sp	splenial	troh	trochlea
s	sternum	sq	squamosal	tu	tuberculum
s c p	subcapsular process	t c	temporal canal	t m	tympanic membrane
s t f	subtemporal fenestra	t	tibia	t r	tympanic ridge
s f	supracoracoid foramen	to	tooth	u	ulna
s o	supraoccipital	t p	transverse process	ul	ulnare
s fe	supratemporal fenestra	ts 1-6	transverse sections one to six	v	vomer
sur	surangular				
su	suture	tro	trochanter		

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