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# THE MORPHOLOGY AND RELATIONSHIPS OF *YOUNGINA CAPENSIS* BROOM AND *PROLACERTA BROOMI* PARRINGTON

by
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## ABSTRACT

Comprehensive descriptions of the osteology of *Youngina capensis* Broom and *Prolacerta broomi* Parrington are presented. New details of the braincase of *Proterosuchus fergusi* Broom are given as these became necessary for comparative purposes. It is suggested that the initial radiation of sauropsid reptiles was a Permian event as yet poorly documented. The phylogenetic position of *Youngina* both forward and backward in time cannot be narrowly defined, though certain characters seem specifically to preclude it from lizard ancestry. *Prolacerta*, on the basis of tooth implantation, braincase morphology and postcranial anatomy is shown to be closest to the proterosuchian thecodonts. It is very definitely not concerned with lizard origins, but would on available evidence seem to be a perfectly good ancestor for the middle Triassic forms *Macrocnemus* and *Tanystropheus*, which latter must cease to be regarded as lizard ancestors. We have here a rather distinct reptilian lineage which branched off from common ancestral stock just prior to the advent of archosaurs.

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## INTRODUCTION

The Permian eosuchians, typified by *Youngina*, are generally considered the hub of later diapsid reptilian diversification (e.g. Romer, 1956).

*Youngina* is relatively poorly known; thus part of the present study will describe the anatomy of this animal in detail. To begin with it will be necessary to decide just what we mean by Eosuchia and to try to decide what is to be understood as comprising the genus *Youngina*. Here it is necessary to be very explicit as it is becoming clear that the Upper Permian was a crucial period in sauropsid evolution and that relationships are not as generalised as has until now been believed.

The Eosuchia are an order within the Subclass Lepidosauria and in the light of the present study must be added to Romer's (1956) otherwise satisfactory definition that dorsal dermal armour was present. The genera comprising Romer's family Younginidae are a reasonably homogeneous group, with the exception of *Noteosuchus*, which shows rhynchocephalian affinities (Carroll, pers. com.). Of the rest the best material in existence is that of *Youngina* (with its taxonomic variants), and these with their smooth peg-like marginal dentition can be distinguished from *Heleosaurus* (Carroll, in press) which has serrated marginal dentition and certain other features which put it more closely in line with the Archosaurs.

Broom (1914 et seq.) was responsible for the three generic and five specific names with which what is manifestly one form (*Youngina capensis*) is presently encumbered. This string of names is misleading; all the specimens come from the same horizon, differing only in size, state of preservation and preparation, and nature of deformation, which factors adequately account for all supposed taxonomic differences. One can have no doubts about synonymising them all under *Youngina capensis* to stress the probability that this was a single monospecific genus. This work will present a detailed description of this animal based on all useful material.

*Prolacerta* (Parrington, 1935), on the basis of its incomplete lower temporal bar, has been considered to represent a stage between the Eosuchia and the Squamata, but this concept must be rejected. A critical re-examination of the true position of *Prolacerta* is necessary. Until now *Prolacerta* (which includes *Pricea*) has been known from a few skulls and some cervical vertebrae. Largely on the basis of an incomplete lower temporal bar it has been regarded as ancestral to the Squamata. The present study describes the whole skeleton and the animal is shown to be Archosaurian in almost every respect.

The braincase of *Proterosuchus* is here re-described in some detail for comparative purposes.

## YOUNGINA

### MATERIAL AND METHODS

The descriptions of *Youngina* are based on material in the Bernard Price Institute (BPI) and one partial skull from the Transvaal Museum (TM). The several specimens in the Rubidge Collection (RC) were examined. Professor Crompton kindly provided copies of his unpublished drawings of *Youngina rubidgei;* these, though useful, have not been used here, and there are one or two points where we differ. These points of difference are those which it has been possible to prepare more fully. A cast and photographs of the Chicago specimen (*Youngoides romeri*) were made available to the author.

All *Youngina* material comes from the *Daptocephalus* zone of the Karroo. The state of preservation is rather different from that of the millerettids (Gow, 1972) of the same age, which might imply some ecological differences in life. While the millerettids are articulated and distortion free, the younginids are disarticulated and the skulls are distorted.

Most of the *Youngina* material has in the past been subjected to mechanical preparation which had caused some damage and also restricted the scope of further work. Fortunately it was possible to prepare a good braincase and skeleton in formic acid; other details were pieced together from mechanical preparation of selected areas of different skulls.

Material referable to *Youngina capensis* Broom 1914.

A.M.N.H. 5561 : *Youngina capensis* Broom 1914. Skull and vertebrae, in American Museum of Natural History.
Locality : New Bethesda, Graaff-Reinet.
Collected : R. Broom.

U.C. 1528 : *Youngoides romeri* Olson and Broom 1937. Skull in University of Chicago.
Locality : Towerwater, Murraysburg.

R.C. 90 : *Youngopsis rubidgei* Broom and Robinson 1948. Very good skull.
Locality : Doornkloof, Graaff-Reinet.
Collected : J. W. Kitching, 1939.

R. C. 91 : *Youngoides minor* Broom and Robinson 1948. A poor partial skull. A second undescribed specimen with the same number is also *Youngina*.
Locality : New Bethesda, Graaff-Reinet.
Collected : Kitching Bros., 1940.

T.M. 1490 : *Youngopsis kitchingi* Broom 1937. A very poor skull.
Locality : New Bethesda, Graaff-Reinet.
Collected : J. W. Kitching.

T.M. 200 : *Youngina capensis* Broom 1922. Fragments of postcranial skeleton, now even fewer than when described by Broom, but certainly of *Youngina*.
Locality : New Bethesda, Graaff-Reinet.
Collected : I. Venter, circa 1920.

T.M. 3603 : Posterior half of a large skull, now acid prepared.
No catalogue data.

R.C. 625 and 626 : Two poorly preserved skulls.
Locality : Wellwood, Graaff-Reinet.
Collected : S. H. Rubidge, 1936—45.

R.C. 714 : Incomplete skull.
Locality : Ganora, New Bethesda, Graaff-Reinet.
Collected : S. H. Rubidge, 1940.

K. 106 : Badly flattened skull in the collections of the Geological Survey, Pretoria.
Locality : Blaaukranz.
Collected : A. W. Keyser.

B.P.I. 375 : Skull.
Locality : von der Waltzhoek, Graaff-Reinet.
Collected : J. W. Kitching, 1946.

B.P.I. 2459 : Small flattened partial skull.
Locality : Klipplaat, Richmond.
Collected : J. W. Kitching, 1951.

B.P.I. 2871 : Skull.
Locality : Beeldhouersfontein, Murraysburg.
Collected : J. W. Kitching, 1958.

B.P.I. 2859 : Skull and skeleton.
Locality : Doornplaas, Graaff-Reinet.
Collected : J. W. Kitching, 1964.

## OSTEOLOGY OF *YOUNGINA*

### The Skull

*Dermal bones of the skull roof*

*Premaxilla* (Figures 1 and 6). The premaxilla is fairly well represented only in B.P.I. 2871. There

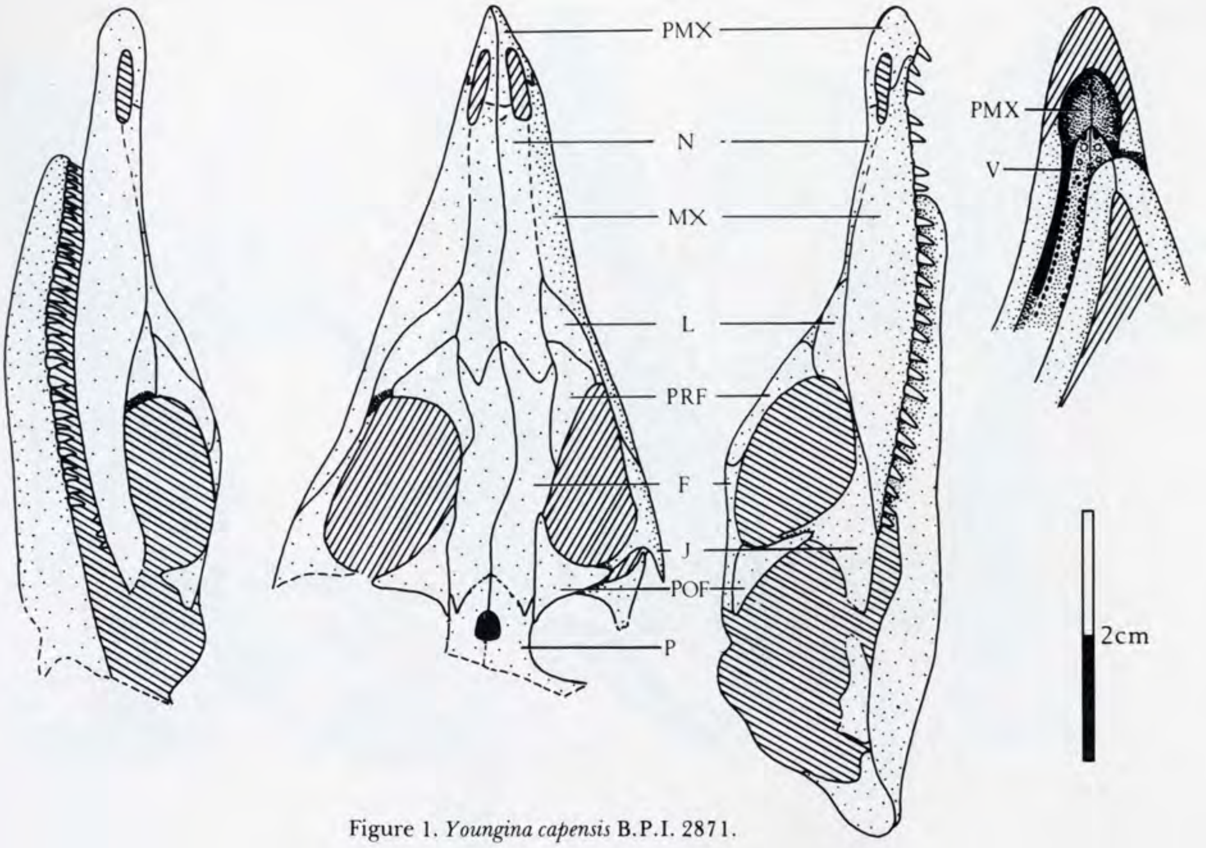


Figure 1. *Youngina capensis* B.P.I. 2871.

appear to have been three premaxillary teeth. The important feature of the premaxilla is its medial extent in the palate: the premaxillae run well back inside the maxillae in a strong contact and meet in the midline.

*Maxilla* (Most Figures). The maxilla sheaths most of the slender, rather shallow snout, and has an extensive contact with the palatine. The teeth are conical, sharply pointed and not serrated; they thicken lingually at the base much as described for *Milleretta* (Gow, 1972); they are sub-thecodont and become firmly ankylosed in deep pits. An exact count is not possible but there are about 30 tooth positions with alternate replacement so that one gets a count of about 20 functional teeth of different ages. An important aspect of the maxillary tooth row is that it extends back to below the postorbital bar (c.f. *Proterosuchus* Cruickshank, 1972, and crocodilians, but not lizards).

*Septomaxilla.* Details of this bone are totally lacking.

*Nasal* (Figures 1 and 6). The relationships of the nasals are clear except anteriorly where there is some doubt as to the exact position of the sutures with the premaxillae, but this is of little consequence.

*Lacrimal* (Figures 1 and 6). The lateral exposure of the lacrimal is reduced to a short distance in front of the orbit. A single foramen runs the full antorbital extent of the bone (as seen in section in R.C. 625).

*Prefrontal.* As figured, requires no special description.

*Frontal* (Figures 2 and 6). The frontals are the only skull roofing elements which have roughened surfaces, notably between the postfrontals and above the orbits. The frontals are rigidly sutured to the parietals.

*Parietal* (Figures 2, 4, 5 and 6). The parietals enclose a large pineal opening and send out posterolaterally directed wings. The area bordering the upper temporal opening is deep and has a shallow pocket in the posterior corner affording a strong area of origin for part of the jaw adductor muscle complex. The wings are joined by a slight ridge between skull table and occiput. Each lateral wing forms important attachments; anteriorly there is an extensive firm contact with the squamosal (Figures 4 and 6): applied to the posterior surface are a post-parietal and tabular, while the tip is sheathed by a supratemporal whose exact relationships will be discussed separately. The lateral wings roof large post-temporal fossae and there is no firm contact with the supraoccipital.

*Postfrontal.* The postfrontal is firmly sutured between frontal and postorbital.

*Postorbital.* The postorbital is overlapped above by the post-frontal (this region, the anterior border of the upper temporal opening, is deep); ventrally it has a rigid sloping contact with the jugal, and posteriorly a broad flat sheet has an extensive overlap onto the squamosal.

*Jugal* (Figures 2, 5 and 6). This is a straightforward element having a long sloping contact with the maxilla and short rigid connections with post-orbital and quadratojugal. Where it forms the anterior border of the lower temporal opening there is a distinctive depression (indicated in Figure 6, lateral view). Internally the jugal has the ectopterygoid abutting against it. It has not been possible to expose the inner surface of this region of the jugal.

*Quadratojugal* (Figures 2 and 6). This is an element

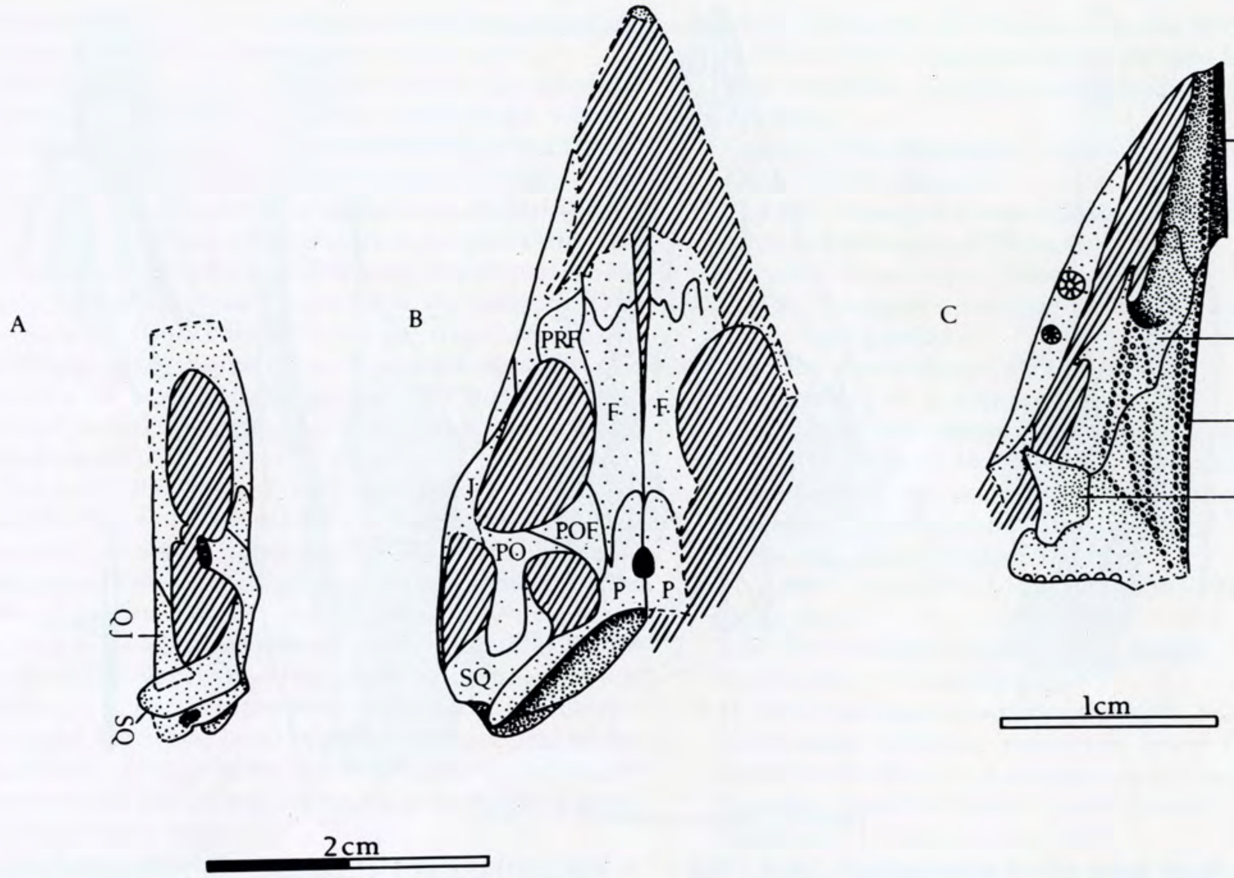


Figure 2. *Youngina capensis* B.P.I. 3859.

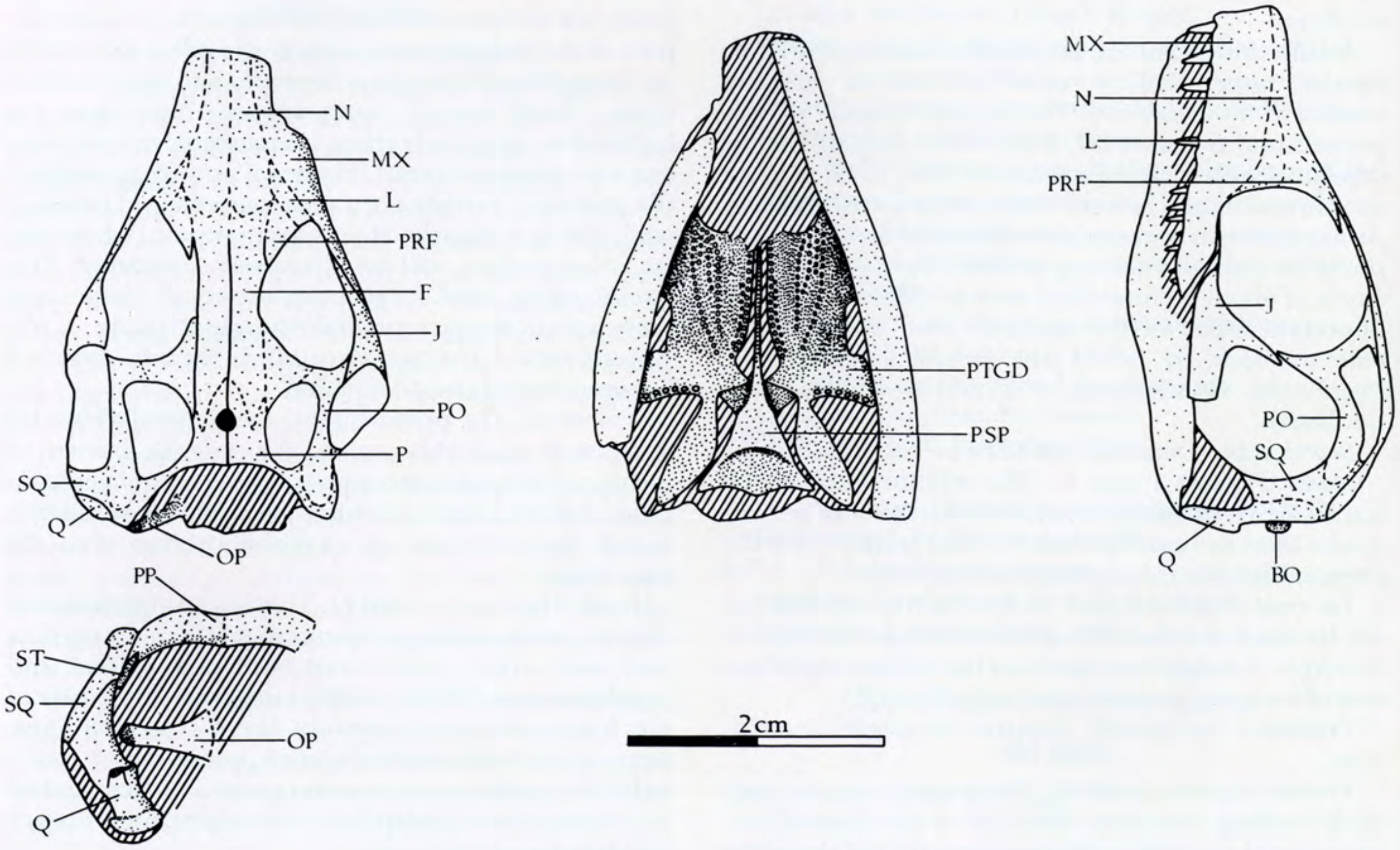


Figure 3. *Youngina capensis* B.P.I. 375.

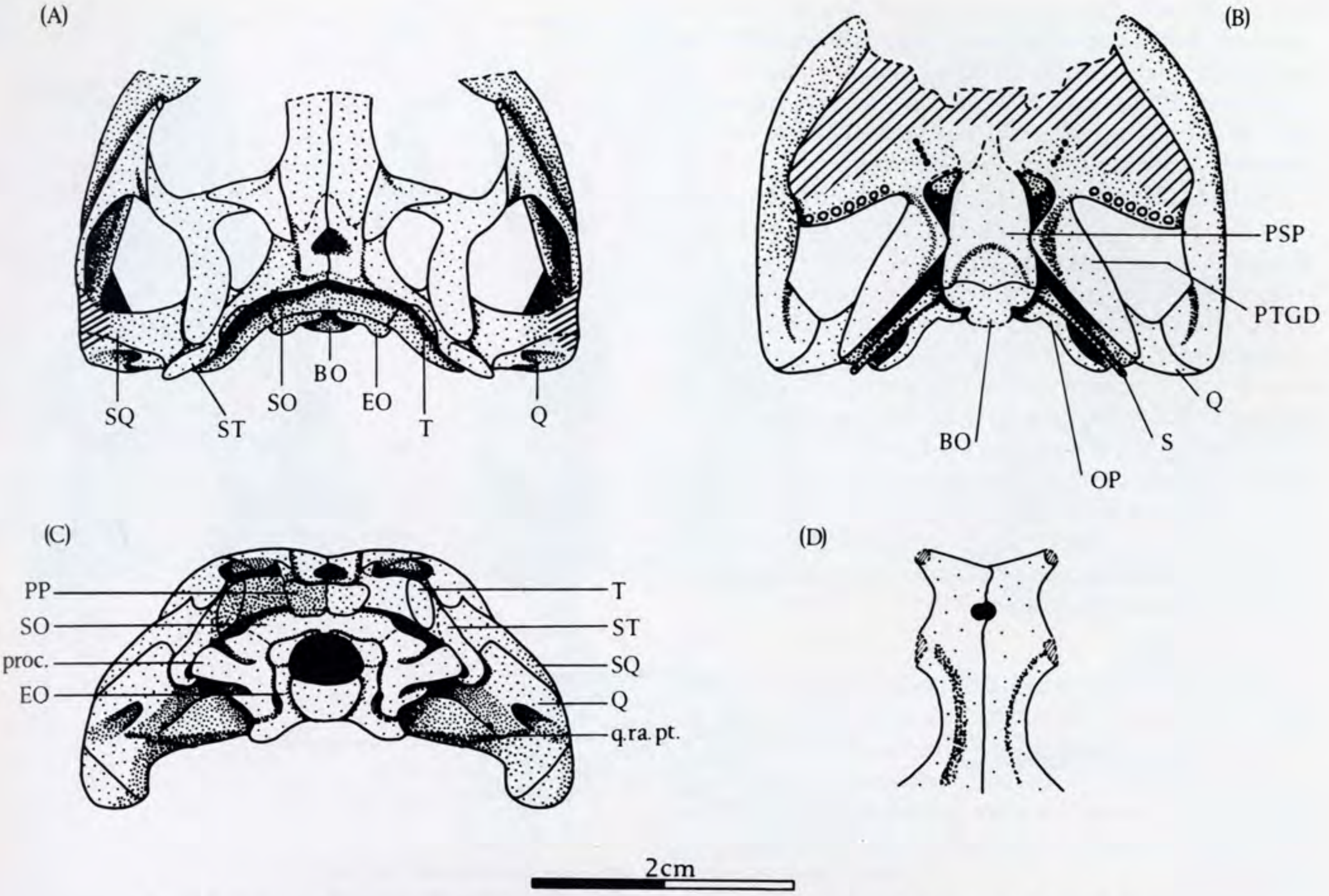


Figure 4. *Youngina capensis* T.M. 3603. A, Dorsal; B, Ventral; C, Occipital; D, Internal detail of frontoparietal region.

critical to phylogenetic discussion. The contact with the jugal presents no problem; it is the relationships to squamosal and quadrate which are important. With B.P.I. 3859 (Figure 2) it was possible to remove part of the squamosal to reveal the full extent of the quadratojugal beneath it. T.M. 3603 provides a check in that the upper two-thirds of the inner surface of the squamosal are clean and there is no sign of any dorsal continuation of the quadratojugal. Unfortunately no specimen shows the contact of quadrate and quadratojugal.

*Squamosal* (Figures 2, 4, 5 and 6). The squamosal overlies part of the quadratojugal below, then rises up in contact with the quadrate, finally turning inwards to cap the quadrate, running under a facet of the postorbital and lapping against the parietal wing.

*Postparietal, Tabular and Supratemporal* (Figures 4, 5 and 6). There is reasonable certainty regarding the presence of these three elements. Postparietal and tabular are simply applied against the back of the parietal. The supratemporal on the other hand is more complex; it lies against the back of the parietal wing and extends beyond its tip, turning down and forwards to form a hook which lies against the top of the pterygoid flange of the quadrate. This hooked supratemporal possibly supported a cartilaginous pad which could rotate against the paroccipital process.

*Sclera.* These are present in B.P.I. 2871 and suggest a ring of ± 12 flat plates.

*The palate.* The palate of *Youngina* has to date been poorly known and imaginatively drawn. Olson's (1936) reconstruction is poor and has been used by Romer (1956): in this, the anterior of the palate is quite wrong as is the epipterygoid stuck in the basal articulation.

*Vomer* (Figures 2 and 6). The vomers are fused in the midline. Anteriorly they disappear above the palatal extensions of the premaxillae which are also united in the midline. Relationships with palatine and pterygoid are clear. Median and lateral borders of each vomer bear a row of small teeth: the median row divides into two along the posterior third of its length. Medial to the tooth rows where the vomers meet they are upturned to form what in palatal view is a narrow smoothly rounded trough. There are two or three larger teeth grouped at the tip of each vomer.

*Palatine* (Figure 2). The relationships of the palatine are clear; it bears four rows of teeth, one a continuation of the lateral row on the vomer, the others of corresponding rows on the palatine. The foot in contact with the maxilla projects downwards somewhat from the level of the palate.

*Ectopterygoid* (Figures 2 and 6). The ectopterygoid overlaps onto the palatal surface of the pterygoid, extending well down the pterygoid flange. This element is poorly known in more primitive reptiles, but by analogy with Millerettids it appears that the infraorbital fenestra in *Youngina* is formed by reduction of the ectopterygoid. The extent of the surface abutting against the jugal is not clear.

*Pterygoid* (Figures 2, 3, 4, 5 and 6). The palatal portion of the pterygoid bears a double row of teeth on the mesial edge continuous with a double row on the vomer. Three rows of teeth fan out from near the basal articulation and continue onto the palatine. The strongly down-turned flange of the pterygoid bears a row of 6 or 7 robust teeth. The articulation with the basisphenoid is freely movable. The quadrate ramus of the pterygoid is a rigid triradiate structure with its edges directed laterally, mesially and dorsally, enclosing a dorso-mesial depression (for the protractor pterygoideus). There is a considerable overlap between pterygoid and quadrate, and a marked supporting ridge on the quadrate.

*The palatoquadrate*

*Epipterygoid* (Figure 5E). Both epipterygoids are partially exposed in T.M. 3603. The upper portion of the shaft is missing; there is no sign of an attachment area on the parietal. A broad footplate rests on the pterygoid very much as illustrated for *Milleretta* (Gow, 1972, Figure 8) and, by analogy, probably caps the basal articulation.

*Quadrate* (Figures 3, 4, 5 and 6). The quadrate is held laterally and dorsally by the squamosal and internally by parietal and supratemporal above and the pterygoid below. Anteriorly it is braced by the quadratojugal. This is a rigid system. The pterygoid ramus is a tall flat sheet. The ridge supporting the quadrate ramus of the pterygoid extends to the back of the quadrate, as is clear from Figures 3, 5 and 6; lateral to this and sloping in from the back of the outer condyle is an abrupt depression. The stapes would have passed across this region. As is plain from the reconstructed lateral view the quadrate is held vertically and the term "otic notch" hardly applies.

*The braincase* (Figure 5)

*Supraoccipital.* The relationships of this element are largely evident from the figures. The supraoccipital runs in under the parietals, this area being bridged by the postparietals. The bone slopes obliquely down and backwards.

*Opisthotic.* The structure and relationships of the opisthotic are clear from the figures. The point to note here is that the paroccipital process articulates in a pocket formed by the supratemporal (Figure 5E).

*Exoccipitals and Basioccipital* (Figures 4, 5 and 6). These form a fused unit. The exoccipitals almost meet above the foramen magnum behind the supraoccipital. The overlap between parasphenoid and basioccipital is clear from Figure 5C.

*Proötic* (Figure 5C, D and E). The region of the fenestra ovalis is poorly ossified (and this is a large specimen), so that the proötic appears suspended from a strong suture with the supraoccipital while ventrally it rests on the basisphenoid. The system of inner ear canals converging at the fenestra ovalis from supraoccipital, opisthosthotic and proötic is well displayed in the specimen.

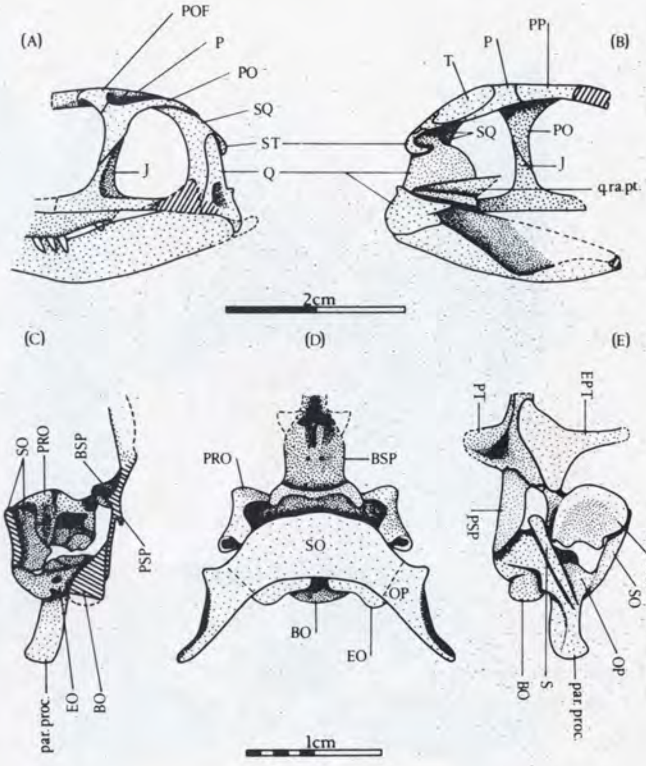


Figure 5. *Youngina capensis* T.M. 3603. A, Lateral view; B. Mesial view of quadrate and cheek region; C, Saggital section through braincase; D, Braincase dorsal view; E, Braincase lateral view.

*Basisphenoid* (Figures 3, 4, 5 and 6). Basisphenoid material is poor. The nature of the basipterygoid processes is clear and the articulation possible here is very similar to that described for millerettids (Gow, 1972); the low clinoid processes too are very similar.

*Parasphenoid* (Figures 3, 4, 5 and 6). The parasphenoid is edentulous. It overlaps the basioccipital extensively and has a pronounced semicircular lip posteroventrally (seen in section in Figure 5C).

*Stapes* (Figure 6). The stapes is a thin rod pierced near the proximal end by a stapedial foramen. The foramen is bounded by an extremely thin bridge which is bowed slightly outwards; such a foramen could well disappear in later forms.

*The lower jaw* (Figure 6)

There is no good lower jaw material: the region of the retroarticular process is eroded off in all specimens. The tooth-bearing rami are rather slender while the region of the adductor fossa is considerably deeper.

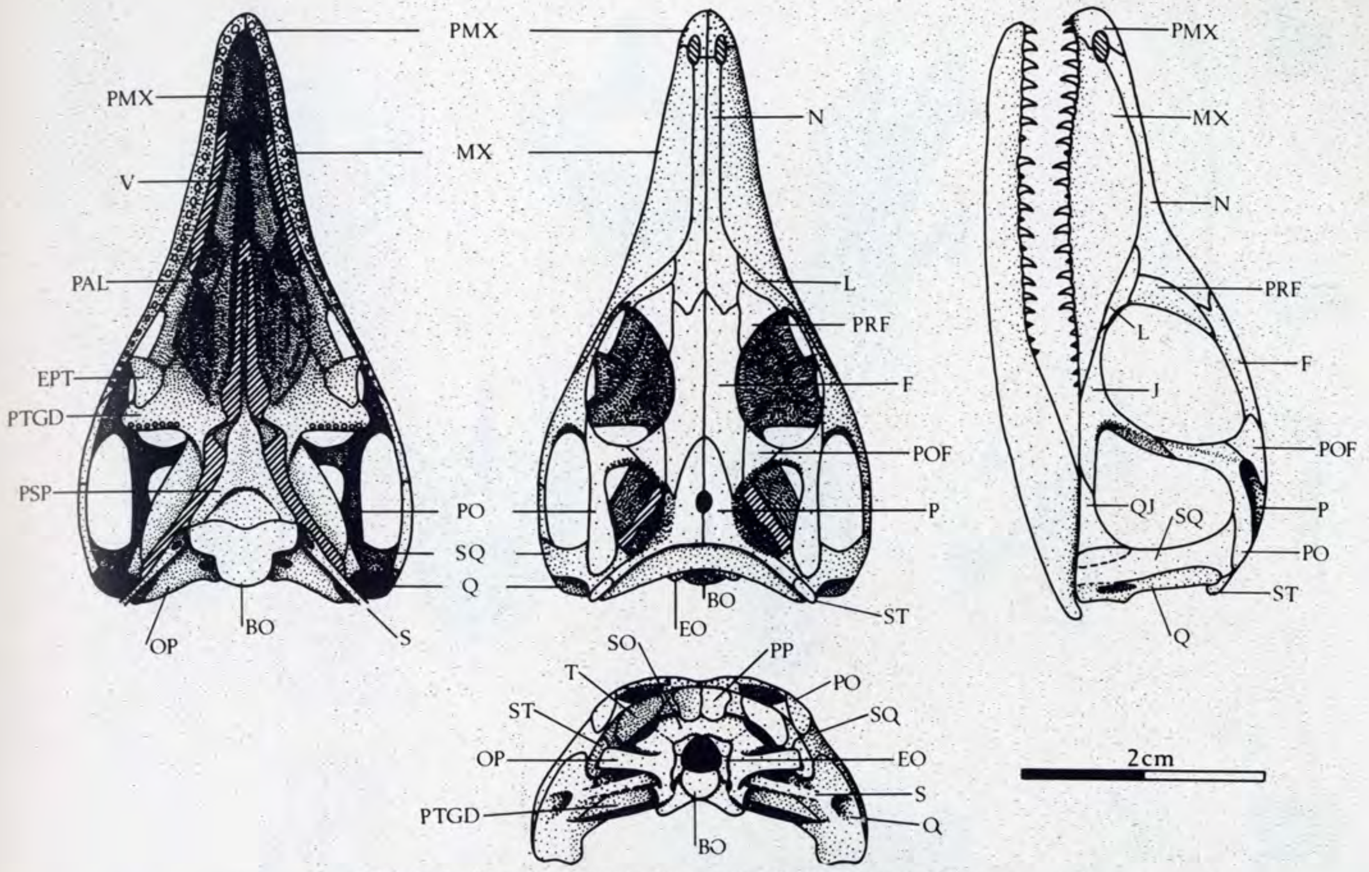


Figure 6. *Youngina capensis.* Composite skull reconstruction.

*The postcranial skeleton of YOUNGINA*

The skeleton of B.P.I. 2859 was jumbled together in a tight bundle behind the skull and part of it had already rotted away. Before acid preparation could commence the skull which had been extensively mechanically prepared had to be removed along a natural joint. The forelimb too was prepared mechanically and removed. The remainder was then disentangled by the repeated use of formic acid. The skeleton comprises a nearly complete set of presacral vertebrae apparently lacking only the atlas, axis and first sacral. The second sacral and first caudal are attached and there are two other caudals and two haemal arches (thought absent by Broom, 1922). There are several plates of middorsal armour. There are several ribs. All elements of both girdles are represented. The left forelimb is complete, also the right humerus. The left femur and the proximal end of the tibia and a presumed fourth metatarsal are all that remain of the hind limb. Thus it is only the hind limb which is incomplete.

*Vertebrae* (Figure 7) *and ribs*

The neural arches are broad and flat with moderately tall spines. The zygapophyses are horizontal, the transverse processes are pronounced, slanted, and have facets for single rib heads. The centra are amphicoelous and notochordal and invisibly fused to the neural arches. Intercentra are present.

The first sacral is missing; in the second the ribs are directed forwards and the distal ends bifurcate, the more anterior branch articulating with the ilium and the posterior branch forming a continuation of the caudal transverse processes and a site of attachment for caudal musculature. The caudal vertebrae with their strong transverse processes and deep haemal arches indicate a deep and powerful tail. A small number of symmetrical middorsal scutes are preserved (Figure 8), sufficient to indicate that there was one to each vertebra but there is no indication as to the extent of the row.

*Girdles and limbs* (Figures 9 and 31)

The pectoral girdle comprises a T-shaped interclavicle (with anteroventral notches for the clavicles), and a scapulocoracoid anteriorly notched to leave a gap between it and the clavicle. The ends of the humerus are rotated at 90° to each other. There is an entepicondylar foramen and a pronounced ectepicondylar groove. Radius and ulna require no additional description. The wrist is practically intact: there is a large ulnare and a rather small radiale, an intermedium, lateral and medial centrales, and five distal carpals. The digits are complete and bear powerful, laterally compressed, curved claws. The pelvic girdle is rather similar to that of *Howesia* (Broom, 1906). The ilium has a short, almost vertical blade, the pubis a pronounced thickened outturned antero-ventral

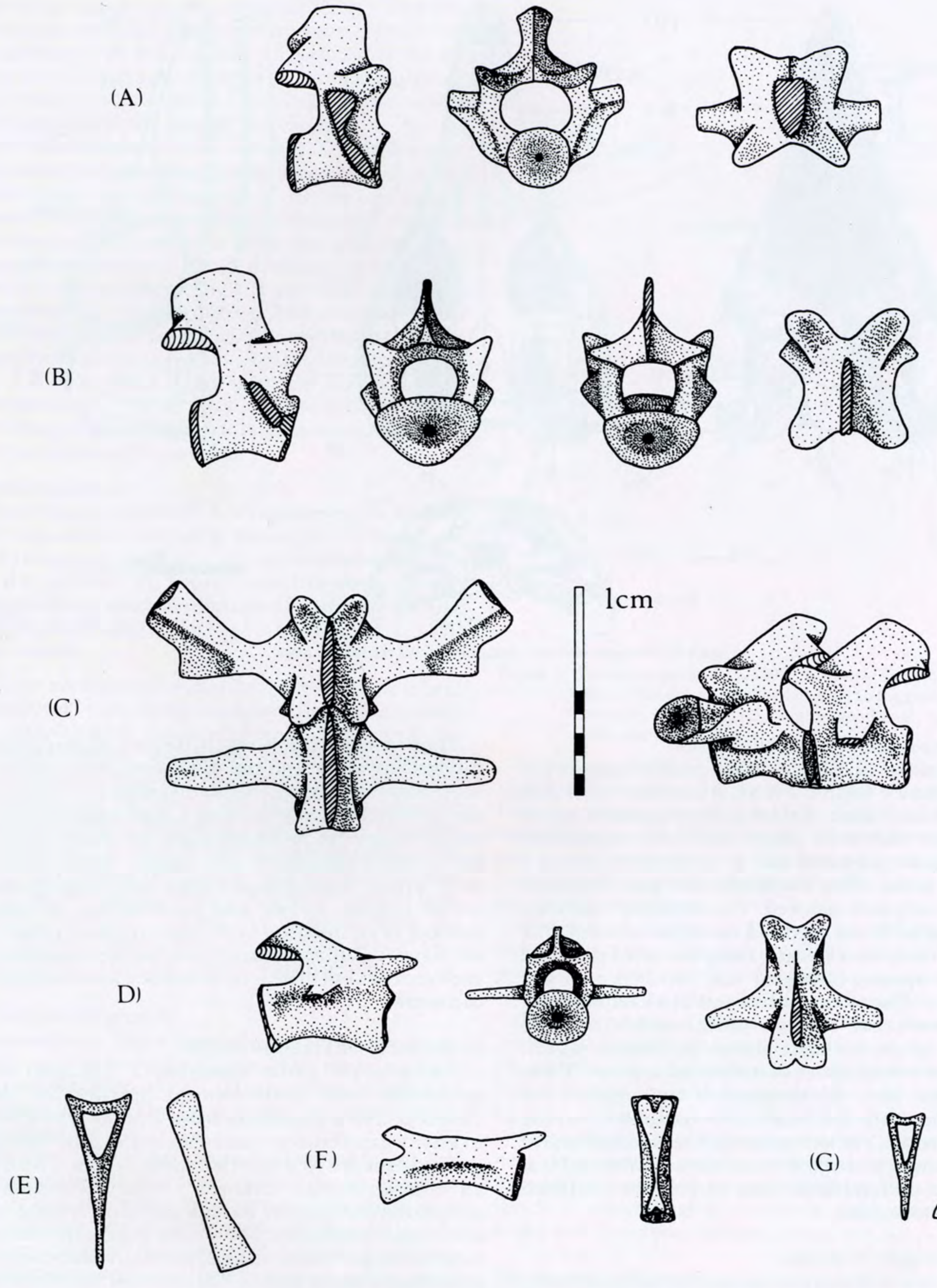


Figure 7. *Youngina capensis* B.P.I. 3859. A, Cervical vertebra; B, Anterior dorsal vertebra; C, Second sacral and first caudal vertebrae; D, Proximal caudal vertebra; E, Proximal haemal arch; F, Distal caudal vertebra; G, Distal haemal arch.
(Cross hatching of neural spines and articular facets does not indicate damaged surfaces.)

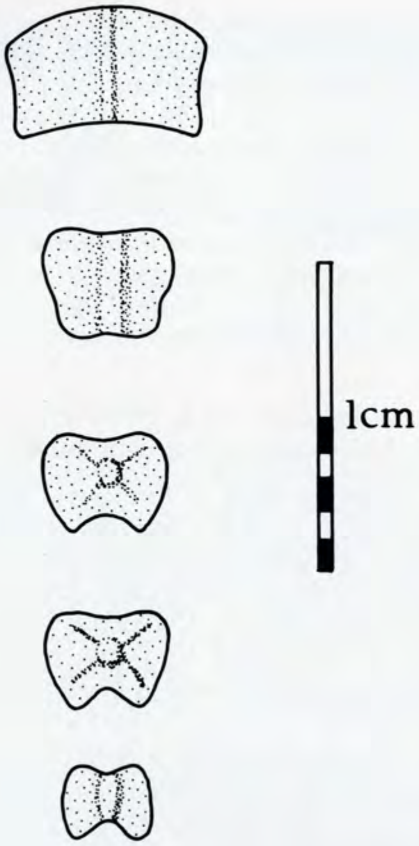


Figure 8. *Youngina capensis* B.P.I. 3859. Mid-dorsal scutes.

process, and the ischium extends well back. The acetabulum is confined to the ilium. The notch between pubis and ischium would, according to Romer (1956, p. 318), indicate incomplete ossification and not an incipient thyroid fenestra.

The femur is primitive, though with a marked curvature which seems natural. The tibia is unfortunately incomplete. There is a single metatarsal which is almost certainly the fourth.

The following are the limb element measurements in mm:

| | | | |
|---|---|---|---|
| Humerus | | | 23 |
| Ulna | 16 | Radius | 18 |
| Femur | | | 34 |

The skeletal fragments described by Broom (1922) were almost certainly correctly assigned to *Youngina,* and as he illustrated a humerus and tibia it is possible to deduce that the femur and tibia were of closely similar length, as shown in the reconstruction (Figure 10).

The ankle described by Broom (1922) is now apparently irretrievably lost, but it is quite clear from Broom's figure and text that it is very like that of early rhynchocephalians and archosaurs.

## *YOUNGINA* FUNCTION

With its long, low, and rather narrow snout, sharp pointed teeth and dermal sculpturing, the *Youngina* skull has a rather crocodilian appearance. Belying this impression are the apparently unspecialised terminal nares.

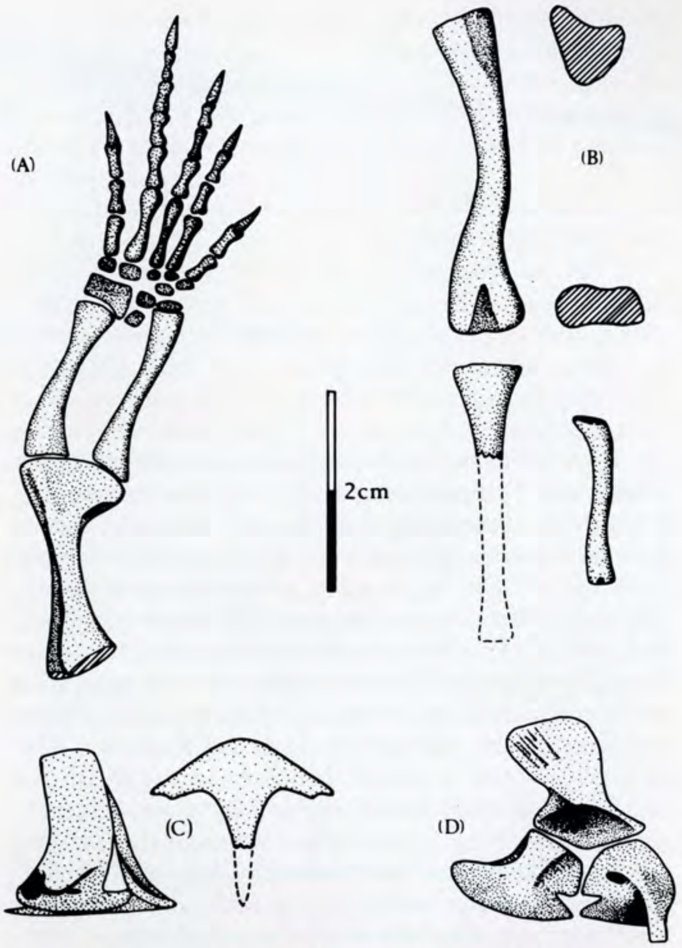


Figure 9. *Youngina capensis* B.P.I. 3859. A, Left forelimb; B, Femur, tibia and fourth metatarsal in anterior view; proximal and distal ends of femur; C, Right aspect of pectoral girdle; D, Right pelvic girdle.

Broom (1922) figured the humerus and tibia of *Youngina;* combining measurements from these with data available from the present study we can conclude with a fair degree of certainty that the tibia was shorter than the femur, but not dramatically so—this points towards a terrestrial quadrupedal existence.

The tail is important, but as the interpretation of tail function is important with *Prolacerta* as well, and as this is a complex and neglected field, some general remarks about tails are in order at this point. Several parameters control the shape and weight distribution of the reptilian tail and some may change according to their position along its length. One may cite: height, breadth and thickness of neural spines; breadth across the transverse processes; position, depth, breadth and thickness of chevrons, and the rate of reduction in size of all the above from root to tip of tail. Clearly a detailed study of tail morphology and function would fill an important gap in present knowledge.

The *Youngina* tail has very low neural spines, which could possibly be simply the retention of a primitive captorhinomorph character. The chevrons on the other hand are long in proportion. Looking for com-

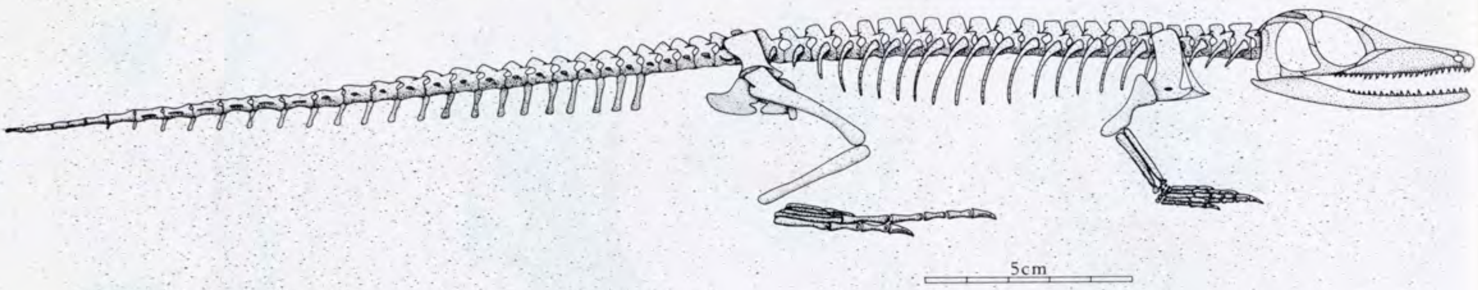


Figure 10. *Youngina capensis.* Reconstruction of the skeleton.

parisons we find that in *Sphenodon* the chevrons are substantial but balanced by tall neural spines. Something closely approaching the *Youngina* condition is seen in one of our local lizards, *Cordylus giganteus*, a fairly large spiky armoured lizard of the grassveld. Pairs live in burrows of their own making, and judging by the even distribution of burrows are strongly territorial. In this animal neural spines are very poorly developed throughout and the chevrons are comparable in size to those of *Youngina.* This similarity of tail structure, however, may be just that and no more, and it is interesting that *Sphenodon* and *C. giganteus* which have more or less the same way of life in several respects should have such different tails. *C. giganteus* would probably fare poorly as a swimmer. This may be a case where it is not possible to explain the observed differences in functional terms.

It should be noted that in swimming reptiles (e.g. crocodiles, monitors) the distal caudal vertebrae have tall neural spines which balance long chevrons in supporting a flattened, more or less symmetrical, tail.

There can be little doubt that *Youngina* was a terrestrial animal. Girdle measurements relating to body sections are given in Table 1.

## *YOUNGINA* RELATIONSHIPS

While the skull of *Youngina* is essentially Permian (braincase, palatal dentition) it exhibits certain advances which foreshadow the Triassic early thecodont grade (considerable palatal extent of premaxillae, suborbital vacuity, and slender stapes). This should not be construed to imply a direct relationship between *Youngina* and a possible *Proterosuchus-Prolacerta* ancestor. These are simply time grades of reptilian evolution, and while it is useful to know what the "Eosuchian" skull looks like there are other small little known U. Permian eosuchians which may prove to be more directly on specific lines to the Triassic Thecodonts (e.g. *Heleosaurus*).

One must concede that the diapsid upper temporal opening is a rigid distinctive feature shared by *Youngina* and its kin plus all later diapsids. The one serious drawback to *Youngina* as a thecodont ancestor is in the structure and relationships of the quadratojugal. Both the tall "archosaurian" quadratojugal of e.g. *Proterosuchus* and the small articulating slip of a bone in *Prolacerta* are readily derivable from the sort of condition seen in millerettids (Gow, 1972, Figures 8 and 22) but not from the arrangement in *Youngina.*

Table 1

| | *Crocodylus niloticus* | *Youngina capensis* | *Sphenodon punctatus* | *Chamaeleo dilepis* | *Prolacerta parringtoni* |
|---|---|---|---|---|---|
| | Measurements in mm. | | | | |
| Interglenoid width IGW | 241 | 28 | 34 | 11 | 32 |
| Interacetabular width IAW | 127 | 19 | 28 | 9 | 30 |
| Pectoral girdle depth<br>Pelvic girdle depth | 178 | 18 | 33 | 18 | 50 |
| Taken together as girdle depth GD | 178 | 22 | 34 | 16 | 46 |
| Ratios | | | | | |
| IGW : IAW | 2:1 | 3:2 | 1:1 | 1:1 | 1:1 |
| IGW : GD | 4:3 | 3:2 | 1:1 | 1:2 | 3:5 |
| IAW : GD | 2:3 | 1:1 | 1:1 | 1:2 | 3:5 |
| Body Shape | Dorsoventrally compressed | | Round bodied | Laterally compressed | |

This is *not* to suggest a relationship between millerettids and thecodonts. This quadratojugal objection does not apply to rhynchocephalian derivation from *Youngina*, but it does reject a too close relationship between rhynchocephalians and early thecodonts.

It seems likely that where the small Permian eosuchians are concerned details of the postcranial skeleton will prove significant in assigning affinities. The girdles and limbs of *Youngina* (the pelvic girdle in particular) are strikingly similar to those of the rhynchocephalian *Howesia* (Broom, 1906).

### *YOUNGINA* — SYNONYMY AND DIAGNOSIS

It is not desirable at this stage to consider the ordinal and familial status of *Youngina*. Future work must decide whether the Order Eosuchia will remain as a depository for unrelated primitive diapsids of doubtful affinity. Certainly several unrelated families are represented in the Younginidae as presently constituted. *Youngina* almost certainly cannot be regarded as more than one palaeontologic species.

Genus *YOUNGINA* Broom (1914 skull, 1922 skeleton)

Species *YOUNGINA CAPENSIS* Broom 1914
= *Youngoides romeri* Olson and Broom 1937
= *Youngopsis kitchingi* Broom 1937
= *Youngopsis rubidgei* Broom and Robinson 1948
= *Youngoides minor* Broom and Robinson 1948

Small upper Permian diapsid reptiles occurring in the *Daptocephalus* zone of the Karroo beds of South Africa. Skull rather shallow snouted with terminal external nares. Some roughening of the frontals particularly above the orbits. Simple plate-like quadratojugal no taller than lower third of quadrate. Postparietals, tabulars and supratemporals present, the latter with ventrally recurved hooks distally for reception of the paroccipital processes. Marginal teeth conical and subthecodont with alternate replacement with approximately 20 functional maxillary teeth. Maxillary tooth row extending well back beneath the orbit. Considerable palatal extent of premaxilla, particularly lateral to the internal choanae. Vomer bearing teeth on both edges, with two or three anterior median "vomerine fangs". Parasphenoid edentulous. Infraorbital fenestra present.

Vertebrae amphicoelous and notochordal with broad flat arches. A middorsal row of scutes, one per vertebra. Second sacral rib bifurcated distally (first not known). Tail with low neural spines and deep haemal arches. Body dorso-ventrally compressed in crocodilian fashion. Proximal limb segments marginally longer than distal.

## PROLACERTA

### REVIEW OF LITERATURE AND MATERIAL

All the *Prolacerta* material comes from the *Lystrosaurus* zone of South Africa of Lower Triassic age. (Colbert has undescribed material of equivalent age collected by Kitching in Antarctica.) *Prolacerta broomi* was first described by Parrington in 1935. Parrington's specimen lacks the posterior spur of the jugal. With this exception, Parrington's reconstruction is good and the specimen is an acceptable type.

Camp (1945) described a second skull and six cervical vertebrae. This is an excellent specimen and Camp's reconstructions are, on the whole, good.

Broom and Robinson (1948) described a third skull as *Pricea longiceps*, but the only respect in which this differs from the previous two skulls is in the nature of its preservation; strikingly different types of preservation of the same species are typical of the *Lystrosaurus* zone, as all familiar with the zone fossils will know.

A fourth skull, in the collections of the South African Museum, Cape Town, has been worked on by Crompton who has kindly given the writer copies of his detailed drawings.

In 1970 Barry Hughes came across some patently sauropsid material in the collections of the Bernard Price Institute; this soon proved to be prolacertid, and the Institute's material can now be listed as follows:

471 Skull *Pricea longiceps* Broom and Robinson 1948.
Locality: Heuning Krans, Burghersdorp.
Collected: J. W. Kitching.
4196 Very small broken and distorted skull in nodule.
Locality: Tweefontein, Bethulie.
Collected: J. W. Kitching.
2675 A skull and skeleton minus sacrum, pelvis, tail and hind legs and including a third scapula.
Locality: Harrismith.
Collected: J. W. Kitching.
2676 An almost complete, articulated postcranial skeleton, lacking the head and first three cervicals.
Locality: Harrismith.
Collected: J. W. Kitching.
4005 Tibia, fibia, ankle and part of foot.
Locality: Old Brickfields Donga, Harrismith.
Collected: J. W. Kitching.

### MATERIAL AND METHODS OF PRESENT STUDY

B.P.I. 2675 was almost completely disarticulated with acetic acid; the skull is now entirely reduced to its elements, and only one hand has been left intact, prepared from one side only. As this took an inordinately long time and as the material is not entirely suited to acid preparation, B.P.I. 2676 was first prepared mechanically in lateral aspect; acid was used on the sacrum and tail which were left articulated, and only the pelvis and hind limbs have been completely cleaned in acid. B.P.I. 4005 was entirely amenable to acid preparation and has been completely cleared of matrix to yield a useful additional ankle. B.P.I. 471, the type of *Pricea*, would be ruined by acid but it has been possible to remove the anterior third of the lower jaws with a saw cut between upper and lower teeth and so to prepare mechanically the anterior of the palate—notably the premaxillae and tips of the vomers. This material then yields the complete osteology of *Prolacerta*.

## OSTEOLOGY OF *PROLACERTA*

### *The skull*

Though the following description refers to B.P.I. 2675, points of difference with the interpretations of other workers are noted.

### *Dermal bones of the skull roof*

*Premaxilla* (Figures 11 and 12). In lateral aspect the premaxilla is somewhat downturned. There appear to be five tooth positions. The premaxillae extend back beyond the tips of the maxillae in the palate and unite in the midline beneath the tips of the vomers.

*Maxilla* (Figures 11, 12, 13, 13A and 32). Figure 13 clearly shows the structure of the maxilla with its thickened tooth-bearing margin dropping away internally to an extremely delicate vertical sheet with internal thickening behind the nasal capsule. The maxilla is excluded from the nasal opening by the premaxilla. There are 25 (+ 2?) maxillary tooth positions and active alternate replacement. The thecodont teeth are laterally compressed, with sharp unserrated edges and are recurved; they are deep rooted, extending the full depth of the thickened alveolar portion of the maxilla which is extremely thin walled.

*Marginal dentition* (Figures 13, 13A and 32). It is essential that the marginal dentition be described in full detail. Thecodont teeth are known in only one group of lizards, the Cretaceous mosasaurs (Edmund, 1967; Russel, D. A., 1967): these teeth are distinguished by having enamel-coated crowns one third the length of the dentine base; resorption pits affect the tooth base and the adjoining bone and arise in the posterior half of the lingual surface of the tooth.

By contrast the teeth of *Prolacerta* appear entirely coated by enamel and are held in deep alveoli by bone of attachment; resorption pits are medially situated in the lingual base of each tooth, and do not affect the adjoining bone of the mandible. In Figure 32A the groove for the dental lamina can be seen clearly, Figure 13A supplements the photographs, giving the pattern of resorption pits and replacement teeth. Among known dentitions this is typical only of the Archosauria.

*Nasal* (Figures 11 and 14). Little can be added to Camp's description. The nasal is overlapped considerably by the maxilla. A clear suture with the frontal is seen in Figure 14A.

*Lacrimal* (Figures 11 and 12). The lacrimal is exposed as a narrow strip on the side of the snout. There are two lacrimal foramina as indicated.

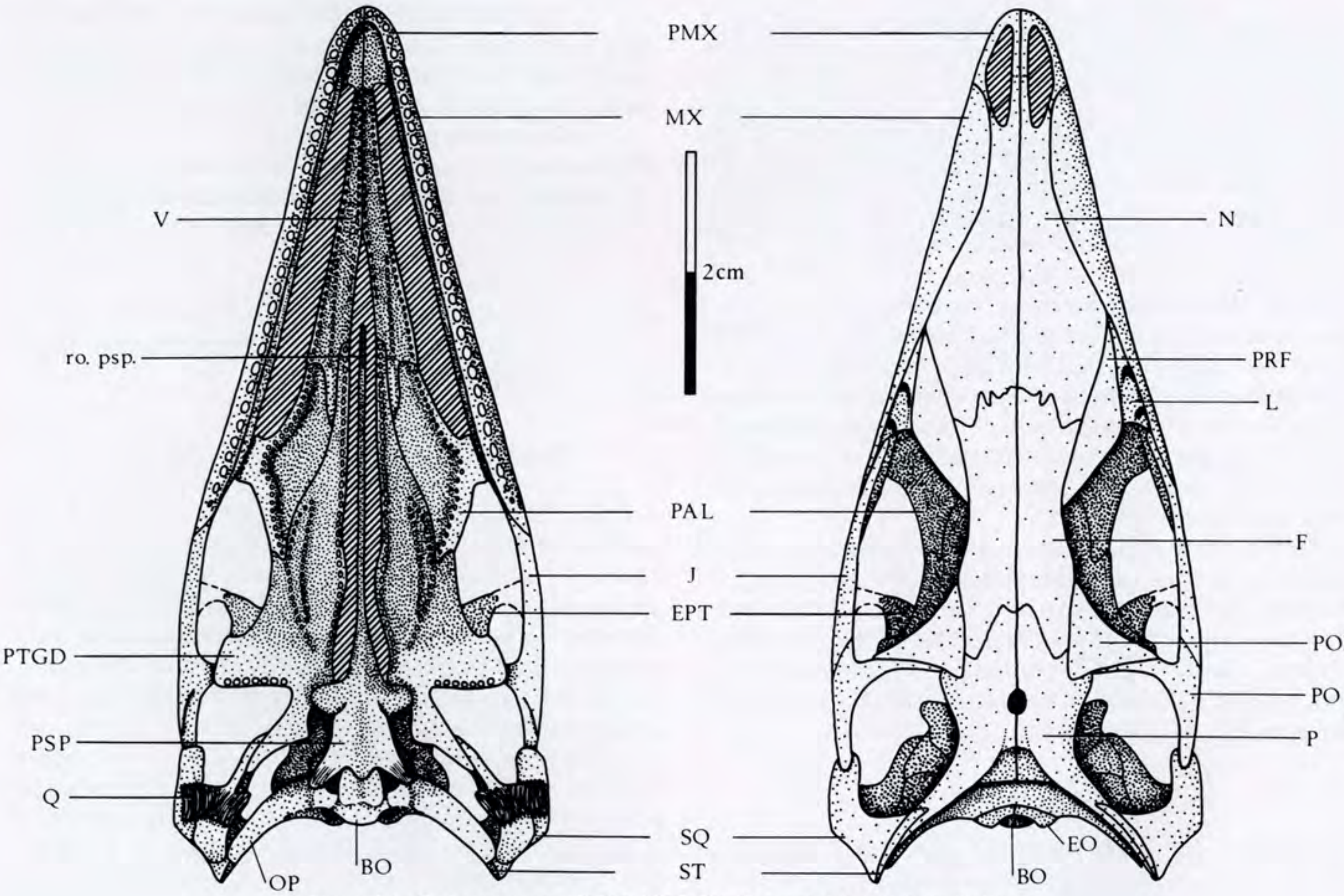


Figure 11. *Prolacerta broomi* B.P.I. 2675. Skull in palatal and dorsal views.

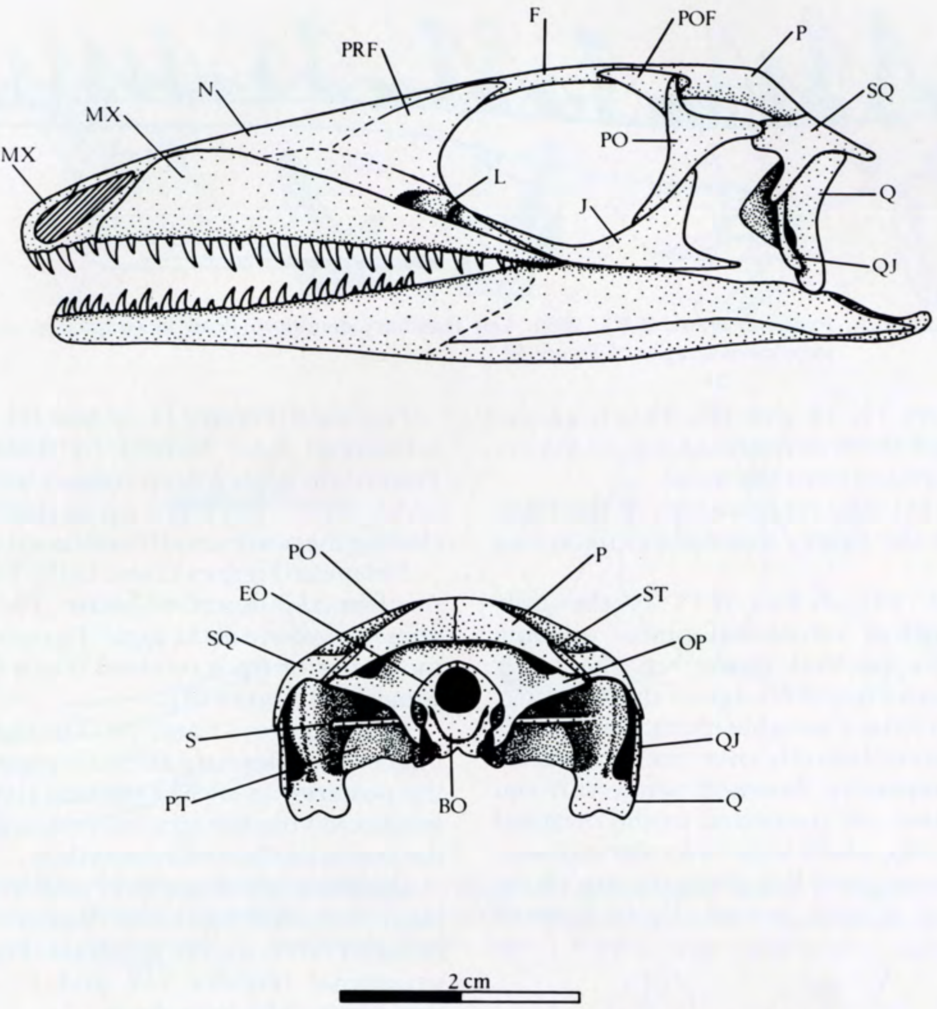


Figure 12. *Prolacerta broomi* B.P.I. 2675. Skull in lateral and occipital views.

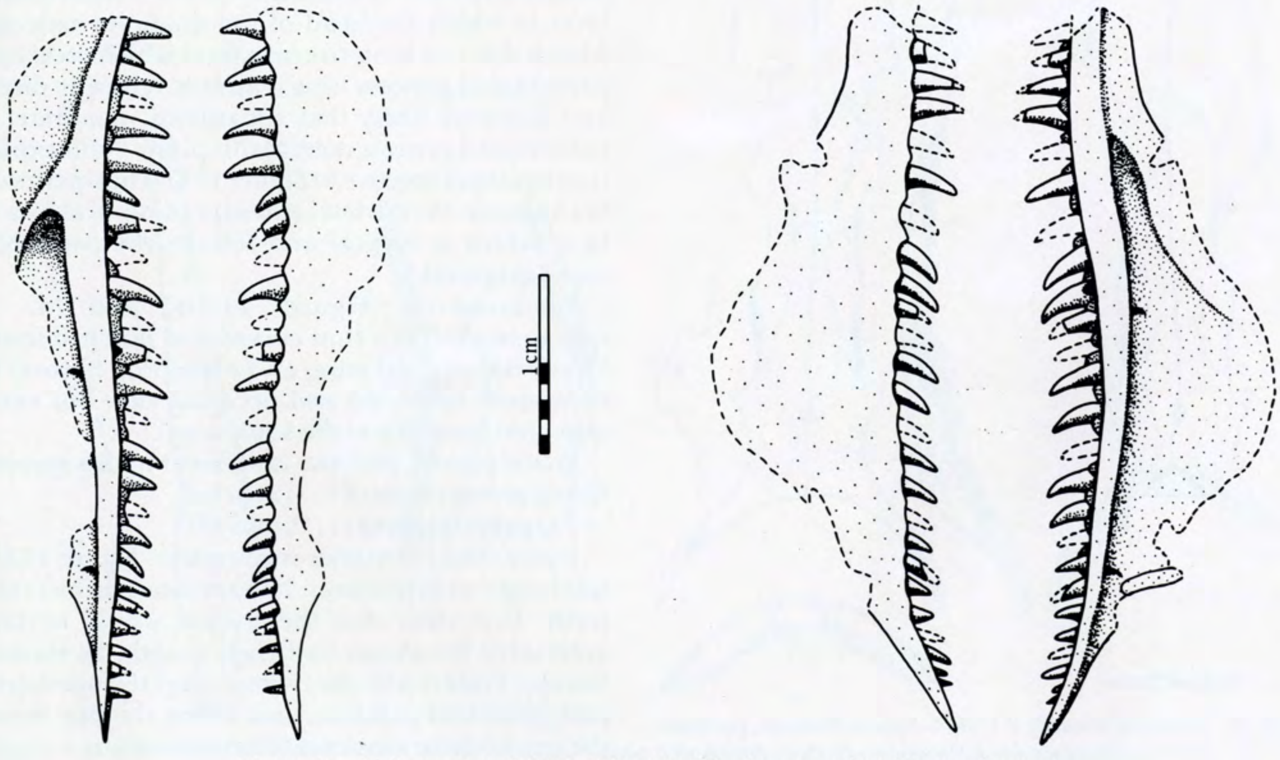


Figure 13. *Prolacerta broomi* B.P.I. 2675. Maxillae in external and internal aspects.

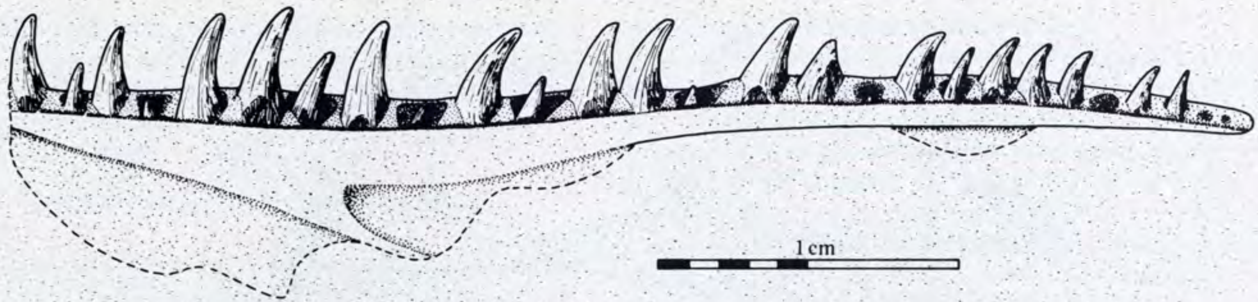


Figure 13A. *Prolacerta broomi* B.P.I. 2675. Left maxillary dentition. Read in conjuction with stereophotographs of Figure 32.

*Prefrontal* (Figures 11, 12 and 14). This is an extremely thin walled element rimming part of the orbit and wrapping round onto the snout.

*Frontal* (Figure 14). The relationships of the frontal are clear from the figure; supraorbital thickening is indicated in C.

*Parietal* (Figure 14). B.P.I. 2675 is the only *Prolacerta* skull with a substantial pineal opening midway along the parietal suture; in the other described specimens there is no sign of this opening; this must be taken to be a variable character. Dorsally the parietals curve laterally over the brain area. Posterolaterally vertically flattened wings run out and back, and these are connected in the occipital plane by a thin bridge which slides over the supraoccipital. The supratemporal lies along the top of the parietal wing and is held proximally in a small notch.

Figure 14. *Prolacerta broomi* B.P.I. 2675. Nasals, frontals, parietals and supratemporals. A, Dorsal (includes prefrontal); B, Left lateral; C, Ventral; D, Occipital.

*Postfrontal* (Figures 11, 12 and 14). This lies against a substantial facet formed by frontal and parietal. Posteriorly it has a deep contact with the postorbital, which latter runs right up against the parietal, excluding the postfrontal from the temporal fossa.

*Postorbital* (Figures 12 and 15G). The contact with the postfrontal is described above. The ventral prong inserts in a groove in the jugal (Figures 15H and I), while the posterior tip is received into a depression on the squamosal (Figure 15E).

*Jugal* (Figures 12 and 15). The right jugal is present intact which clears up all doubt regarding the extent of the posterior spur. The portion rimming the orbit is substantial but the spur and the area above it behind the postorbital are extremely thin.

*Quadratojugal* (Figures 12 and 15). The quadratojugal is a small bent and flattened rod articulating between facets on the quadrate (Figure 15A) and the squamosal (Figures 15E and F), with a foramen between it and the quadrate.

*Squamosal* (Figures 11, 12 and 15). Facets for postorbital and quadratojugal have already been described. Posteriorly there is a mesially directed hemispherical facet in which the head of the quadrate articulates. Above this is a long concave facet which receives the paroccipital process (this is almost ventrally directed and it seems likely that squamosal, quadrate, and paroccipital process meet at this point—this explanation lends perspective to Figure 15F). The squamosal is held against the parietal and supratemporal by a fifth facet which is vertical and follows the curve of the supratemporal.

*Supratemporal* (Figures 11, 12 and 14). The supratemporal is a thin curved rod notched into the top of the parietal wing and extending beyond it: it is exposed in dorsal and occipital view but entirely obscured laterally by the squamosal.

*Scleral plates.* Sclerotics are absent in this specimen. Camp gives a count of 11-12 for his.

*The palate* (Figures 11, 16 and 17)

*Vomer.* The left vomer is complete (Figure 16A) but was lying out of position. It bears three distinct rows of teeth. It is clear that the vomers would be united anteriorly for about half their length, as shown by Camp. Posteriorly the vomer slightly overlaps the pterygoid and palatine, also filling the gap between the tips of these elements (Camp illustrates a gap here but this is improbable).

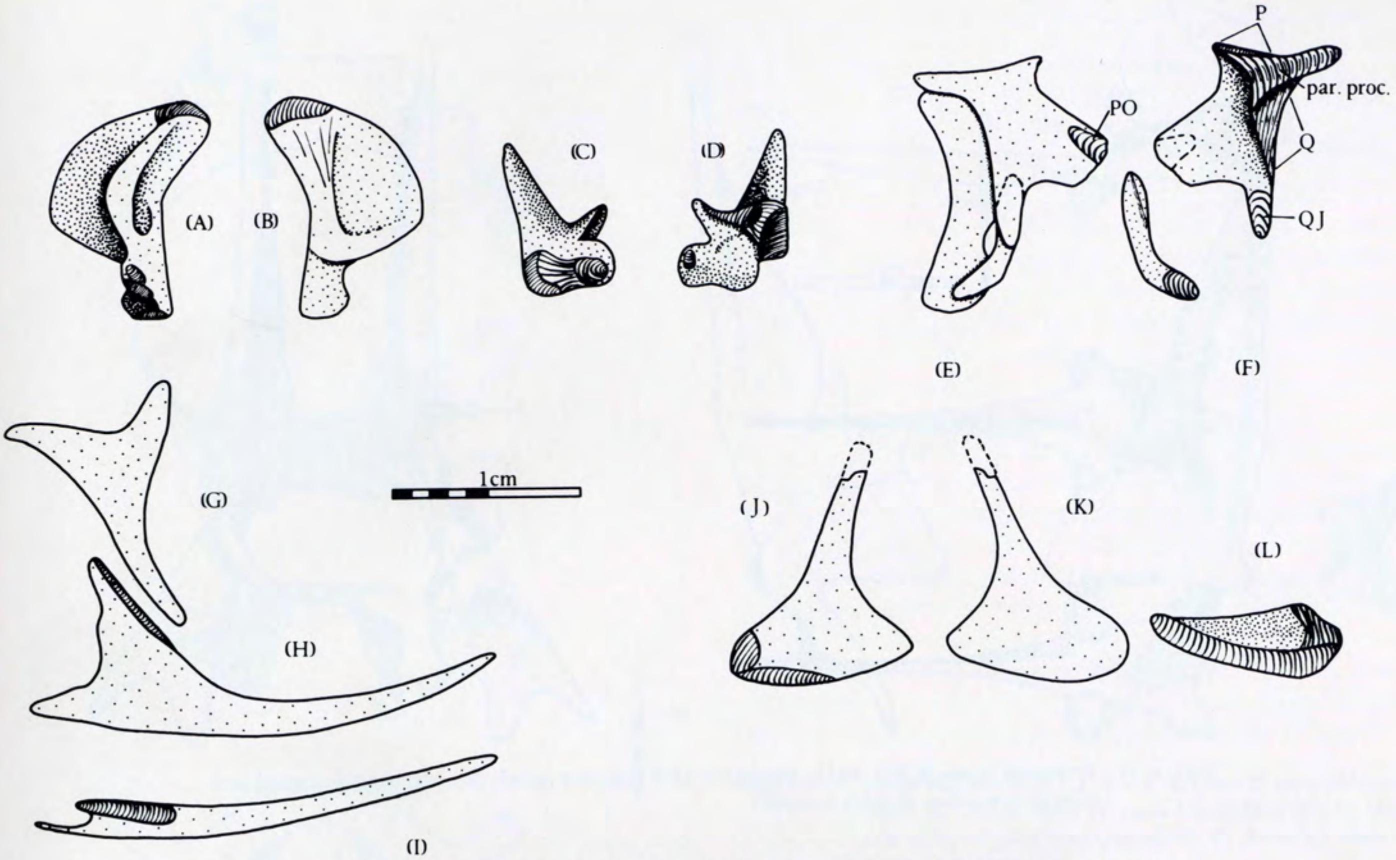


Figure 15. *Prolacerta broomi* B.P.I.2675. A—D, Quadrate; A, Lateral; B, Mesial; C, Ventral; D, Dorsal; E, Squamosal, quadrate and quadratojugal; F, Squamosal in internal aspect and quadratojugal; G, Postorbital; H and I, Jugal; J, K and L, Epipterygoid in lateral, mesial and ventral views.

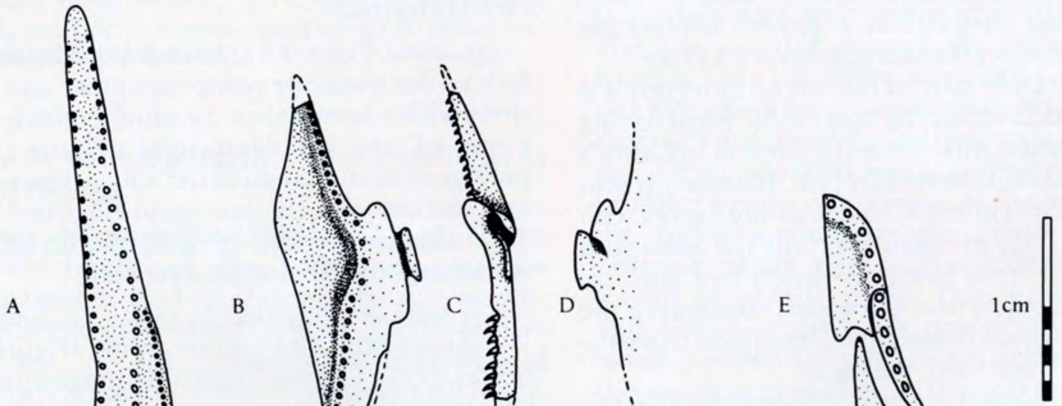


Figure 16. *Prolacerta broomi* B.P.I. 2675. A, Vomer; B, Palatine; C, Palatine in lateral view; D, Dorsal view of palatine foot; E, Palatal extent of premaxilla.

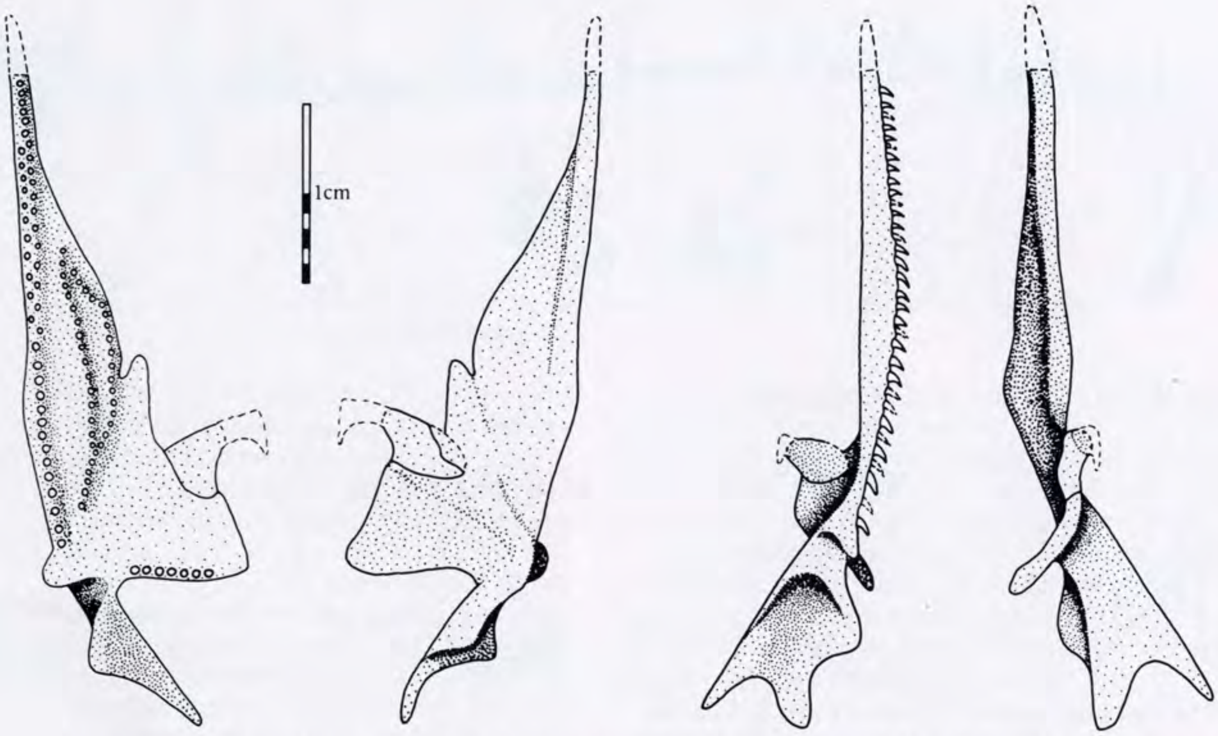


Figure 17. *Prolacerta broomi* B.P.I. 2675. Pterygoid and Ectopterygoid: palatal, dorsal, mesial and lateral views (last slightly rotated).

*Palatine*. The mesial portion of the palatine is an extremely thin sheet; laterally the bone thickens and turns downwards, this thickened edge bearing a single row of teeth continuous with those of pterygoid and vomer. The foot of the palatine is applied against the alveolar border of the maxilla and has a small dorsal process which rests on top of the alveolar ledge (Figure 16B and D). Above this latter process is the palatine groove which transmits the maxillary artery and superior alveolar nerve (Figure 16C) which then enter a foramen in the maxilla (Figure 13), branches also possibly running forward in a groove behind the alveolar ledge to enter the more anterior foramen.

*Ectopterygoid*. Only part of the left ectopterygoid is present, the process abutting against the jugal having been lost. However, this element is present in Camp's specimen and well illustrated by him. It is also present in Crompton's specimen, whose drawing agrees with that of Camp. This element overlaps the pterygoid from above (not from below as shown by Camp); it curves gently forward and outwards, continuing the edge of the pterygoid flange, and terminates in a substantial foot in contact with the jugal.

*Pterygoid*. The palatal portion of the pterygoid is extremely thin, except where it turns up into a ridge bordering the interpterygoid vacuity. On the mesial border there is a continuous row of teeth, while from just anterior to the basal articulation a double row runs towards those of the palatine; the flange is also toothed. A notch on the lateral edge of the pterygoid receives the palatine. The articulation for the basipterygoid process is deep, hemicylindrical, and directed obliquely posteriad. The quadrate ramus is deeply concave on its mesial surface with a pit situated anteriorly. The ornate margins of this process (Figure 17) are genuine. The area of origin of the *pterygomandibularis* is marked by a ridge on the inwardly sloping lower portion of the quadrate ramus.

*Epipterygoid*. The lower half of each epipterygoid is preserved. It is very similar to that of *Youngina*, including a facet capping the basal articulation. Camp's description and figure of a thin quadrate process is clearly an artifact.

*Quadrate* (Figures 11, 12 and 15). The articular surface of the quadrate comprises inner and outer condyles with a facet above the outer condyle for attachment of the quadratojugal (Figure 15A). The pterygoid ramus is extensive, with a depressed area of articulation with the pterygoid (Figure 15B). Figure 15D indicates the areas of cartilaginous attachment to squamosal and paroccipital process.

*The braincase* (Figures 12, 18, 19, 34 and 35).

*Supraoccipital*. The supraoccipital (Figure 18A-D) is broad, as in *Youngina*. There is no suggestion of contact with the parietals; post-temporal fossae were present.

*Opisthotic*. The opisthotic is firmly united to supraoccipital and proötic. Its ventral ramus borders the foramen ovale anteriorly and the jugal foramen mesially. Above the jugal foramen is a facet for the reception of the exoccipital. The ventral ramus has a loose mesial contact with a ventrally directed process of the basioccipital. The paroccipital process is flattened, as in *Varanus*, but meets the squamosal/quadrate

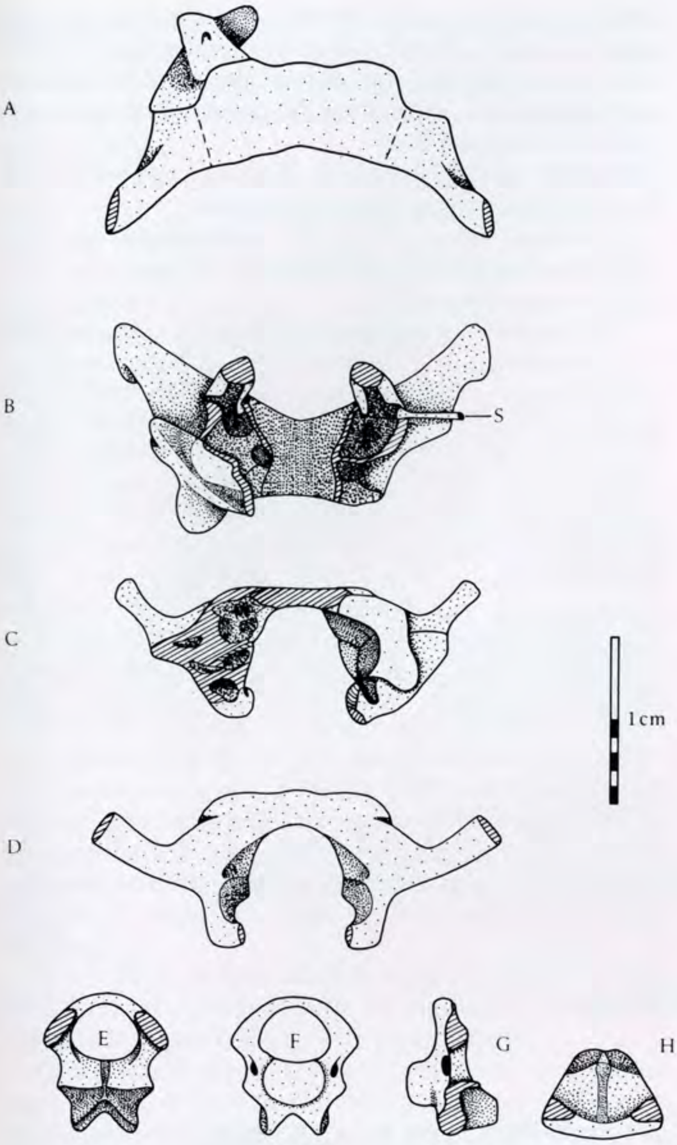


Figure 18. *Prolacerta broomi* B.P.I. 2675. A – D, Supraoccipital, proötic and opisthotic; A, Dorsal; B, Ventral; C, Anterior; D, Posterior; E—G, Basi- and exoccipitals; E, Anterior; F, Posterior; G, Lateral; H, Dorsal (exoccipital ring removed).

joint more or less horizontally, and not vertically as does that of *Varanus*.

*Exoccipital and basioccipital* (Figure 18E-H). These elements are fused and they completely ring the foramen magnum. The braincase is difficult to assemble as so many joints involved cartilage, and this is particularly true of the basioccipital/parasphenoid relationship (Figure 11). These bones separated freely, though it seems the medial prong of the parasphenoid was applied beneath the basioccipital. The lateral prongs of the parasphenoid, however, span the same width as the ventral tips of the opisthotics and it seems very likely that parasphenoid, basioccipital, and opisthotics were held together in cartilage at this point, the basioccipital contributing reasonably discrete basal tubera.

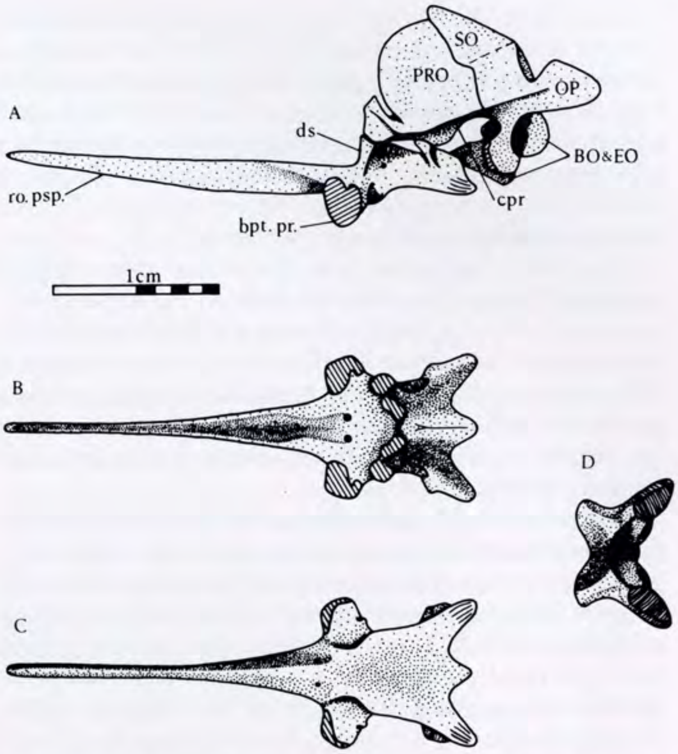


Figure 19. *Prolacerta broomi* B.P.I. 2675. A, Lateral view of braincase; B, Dorsal view of para-basisphenoid; C, Ventral view of para-basisphenoid; D, Anterior view of para-basisphenoid.

Before leaving the occiput it should be noted that Camp's (1945) reconstruction of this area is completely wrong. Robinson's (1966) is better, but the tips of the paroccipital processes are out of position, the tops of the exoccipitals are the wrong shape and do not meet, the top of the quadratojugal is shown touching the outer surface of the squamosal instead of the inner, and the quadrate squamosal contact is too low.

*Proötic* (Figures 18 and 19). The proötic has extensive sutural contact with supraoccipital and opisthotic. The pila antotica contacts the dorsum sella of the basisphenoid and there is an additional ventral contact with a delicate posterior ridge of parasphenoid (cf. description of *Proterosuchus* braincase to follow). There is a deep trigeminal notch and a pronounced crista proötica which continues on to the opisthotic; within the recess formed by the crista and somewhat posterior of the trigeminal notch is a small foramen for the facial (VII) nerve. This is the earliest known appearance of the crista proötica s.s. (see *Youngina*) which is particularly significant as a point of origin for the *protractor pterygoideus*. (Internal canals in supraoccipital, opisthotic and proötic are clearly displayed—should comparison prove necessary.) Medial to the crista proötica is a further depression above the foramen ovale (involving proötic and opisthotic) for the anterior semicircular canal (Oelrich, 1956, p. 15).

*Para/Basisphenoid* (Figures 11 and 19). This element is completely edentulous. The parasphenoid rostrum, V-shaped in cross section, extends a little farther forward than the pterygoids. Posteromedially there is a light overlapping contact with the basioccipital, while posterolaterally a gap exists which, when closed by cartilage, would connect basisphenoid and opisthotic. Prominent basipterygoid processes (orientation Figure 19D) correspond with deep pockets in the pterygoids already described. The vidian (parabasal) canal is a deep groove.

The only foramina are those for the internal carotids. The course of the abducens (VI) is marked by a groove on the posterior dorsal surface between alar process and dorsum sella. The alar process meets the pila antotica, its lateral edge continuous with the crista proötica. Behind the dorsum sella the bony sheet (parasphenoid) is W-shaped in cross section, with tall lateral walls.

The posterolateral extremities of the parasphenoid do not contact the ventral processes of the opisthotics in the region where the sternohyoideus muscles would attach. This area would have been filled in by cartilage. A distinctive ridge on the posterolateral wall of the parasphenoid terminates in a knob which meets the proötic below and in front of the lagena recess. Between this point of contact and the alar process there is a sharp smooth edge of parasphenoid; by contrast the corresponding edge of the proötic is broad and channelled, indicating the presence of a connecting membranous sheet.

*Stapes* (Figures 12 and 18). The stapes is a thin rod, the stapedial foramen having been lost.

*Ceratobranchial.* A long thin ceratobranchial I is present—this has been described by Camp.

*The lower jaw* (Figure 20).

The elements of the lower jaw, like those of the skull, are rather delicate. The Meckelian canal runs to the tip of the dentary. There is a large Meckelian fossa on the lingual surface. The glenoid, with two distinct facets, was probably reinforced anteriorly by a wad of cartilage. The large broad retroarticular process bears muscle attachment scars (*pterygomandibularis*). Twenty-seven tooth positions are indicated, the teeth being somewhat smaller than the maxillary teeth. The symphysis is extremely light and was probably movable. The relationships of the bones are clear from the figures, though some notes are in order. The *surangular* contributes the lateral glenoid facet, and

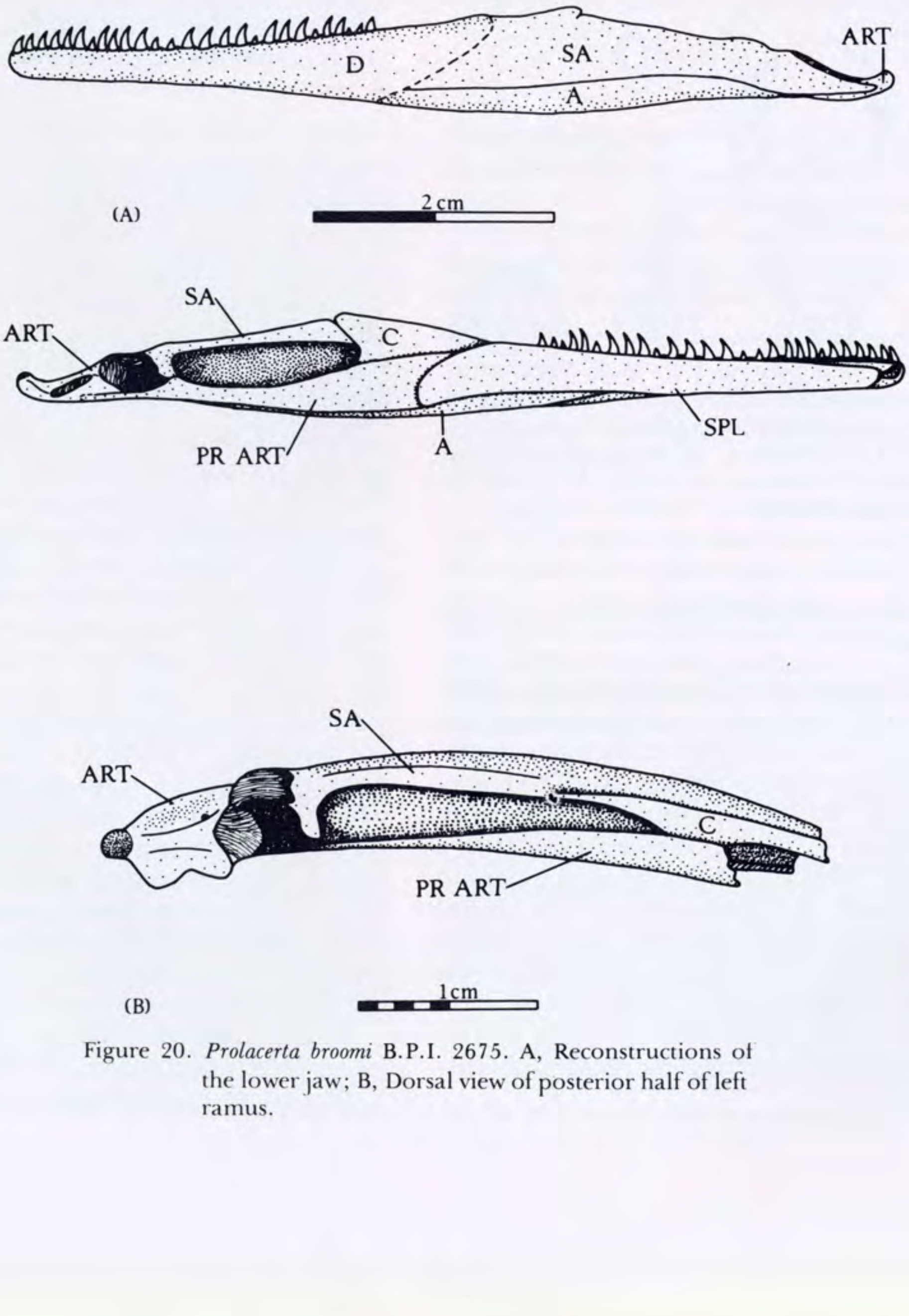


Figure 20. *Prolacerta broomi* B.P.I. 2675. A, Reconstructions of the lower jaw; B, Dorsal view of posterior half of left ramus.

sends a projection mesially to contact the prearticular.

The *angular*, which forms the postero-ventral border of the jaw, terminates beneath the glenoid. The tip of the *coronoid* is barely raised above the dorsal surface of the jaw.

The *articular* contributes the mesial glenoid facet; its recurved tip forms the site of attachment for the *depressor mandibularis*. There is good evidence for a tympanic crest on the lateral border. The chorda tympani/posterior condylar artery foramen is present. There is an incipient angular process.

### *The postcranial skeleton*

The nearly complete articulated skeleton, B.P.I. 2676, lacks the first three cervicals and of the forelimbs only the proximal ends of the humeri are present. B.P.I. 2675 which contains the forelimbs and skull is truncated anterior to the pelvis. The overlap between these two specimens then is only in the vertebral column and the scapulocoracoids.

It must be stated at the outset that scales in the drawings are true for the smaller specimen (B.P.I. 2675) while the larger specimen has been reduced by 1/6th to bring it to the same size: this figure was arrived at by measuring the scapulocoracoids and this reduction produced a very good fit of the vertebrae. While this appears to be satisfactory it is unfortunate that an approximation was necessary, though the critical proportions of the skeleton are of a far greater order of magnitude than any error of scale which may have resulted.

B.P.I. 4005 yielded additional information on the hindlimb, and here there is no problem of equating size with undistorted tibiae for comparison.

Camp has described the first six cervical vertebrae and suggested they might indicate aquatic habits—a significant remark in view of the close affinity of bipedal lizards for water (Neill, 1971). *Prolacerta* was clearly a bipedal runner with a large tail to counterbalance the weight of the body. That the head and neck were highly manoeuvrable is shown by thickening of the tips of the neural spines in the shoulder region. Like the skull, the skeleton is extremely light, with hollow limb bones, and centra thin walled but supported by a delicate web of internal bony struts (there is no sign of pneumatopores). The ankle and hooked fifth metatarsal are similar to those of rhynchocephalians and *Proterosuchus*, yet not much different from those of *Euparkeria*. Intercentra are one primitive character in an otherwise very advanced, typically Triassic, skeleton.

The whole animal is so closely comparable to *Macrocnemus* (Peyer, 1937; Kuhn Schyder, 1962) as to assure very close relationship. It seems ridiculous to think of these distinctive thecodonts as lizards: they are yet another group which has dispensed with the lower temporal arcade. *Glevosaurus hudsoni* (Robinson, 1973) is an undoubted sphenodontid which has an incomplete lower temporal arcade. Clearly this feature evolved independently in squamates, thecodonts and rhynchocephalia.

### *Axial skeleton*

There are 26 presacral vertebrae, including proatlas, deeply amphicoelous but not notochordal. There are two sacrals and a string of 13 proximal caudals plus several isolated more terminal caudals. Intercentra are present only as far back as between the first two caudals, after which they are succeeded by very long, flat haemal arches. The vertebrae are very lightly constructed: there is no sign of separation between centrum and neural arch; the centra are hollow with an intricate system of internal supporting struts.

*Atlas and axis* (Figure 21). The atlas complex is primitive. The proatlas connects the atlas arch to the exoccipital above the foramen magnum. The paired atlas arch elements just meet in the midline anteriorly and rest on a large pleurocentrum. The atlas intercentrum articulates between the occipital condyle and the axis intercentrum. This gives the appearance of being a highly mobile joint. The axis has a long neural spine typical of this bone, and it has a facet for the first cervical rib.

*Cervicals* (Figure 21, (7)). The following six vertebrae may be termed cervicals; they are greatly elongated. The last three cervicals and first three dorsals have thickened neural spines—clearly points of attachment for important neck muscles. In the neck region capitular facets are all on the centra and do not involve the intercentra. Rather long, slightly inclined zygapophyses would permit great freedom of movement, both lateral and dorsoventral.

*Anterior dorsals.* A lateral ridge leading towards the tubercular facet becomes increasingly pronounced posteriad until the first dorsal, which is characterized by transverse processes with their leading edges almost at right angles to the column (Figure 21, (10)). The length of the neural spines decreases to a minimum on 10 before picking up again over the back. This is also the point at which the rib facets start to merge, forming a continuous articular region. This process is complete by 15.

*Posterior dorsals.* Here there is a slight but distinct alternation in the length of the neural spines. By 19 all trace of two rib facets has gone leaving a single circular facet (Figure 22, (21)).

*Sacrals* (Figure 22). The narrow-necked transverse processes (or pleurapophyses) widen into substantial facets which touch and interlock slightly as shown. The transverse processes of the second sacral bifurcate into two functionally distinct processes; the anterior process is thick and broad and abuts against the ilium. The posterior process is thin and narrow and does not touch the ilium; it in fact constitutes an additional caudal transverse process and would no doubt strengthen the attachment of tail muscles, helping to support and control the large powerful tail which is such an important organ to a bipedal lizard-like animal. (This seems to be a rather different arrangement from that described for *Proterosuchus* by Cruickshank, though I am not convinced that the

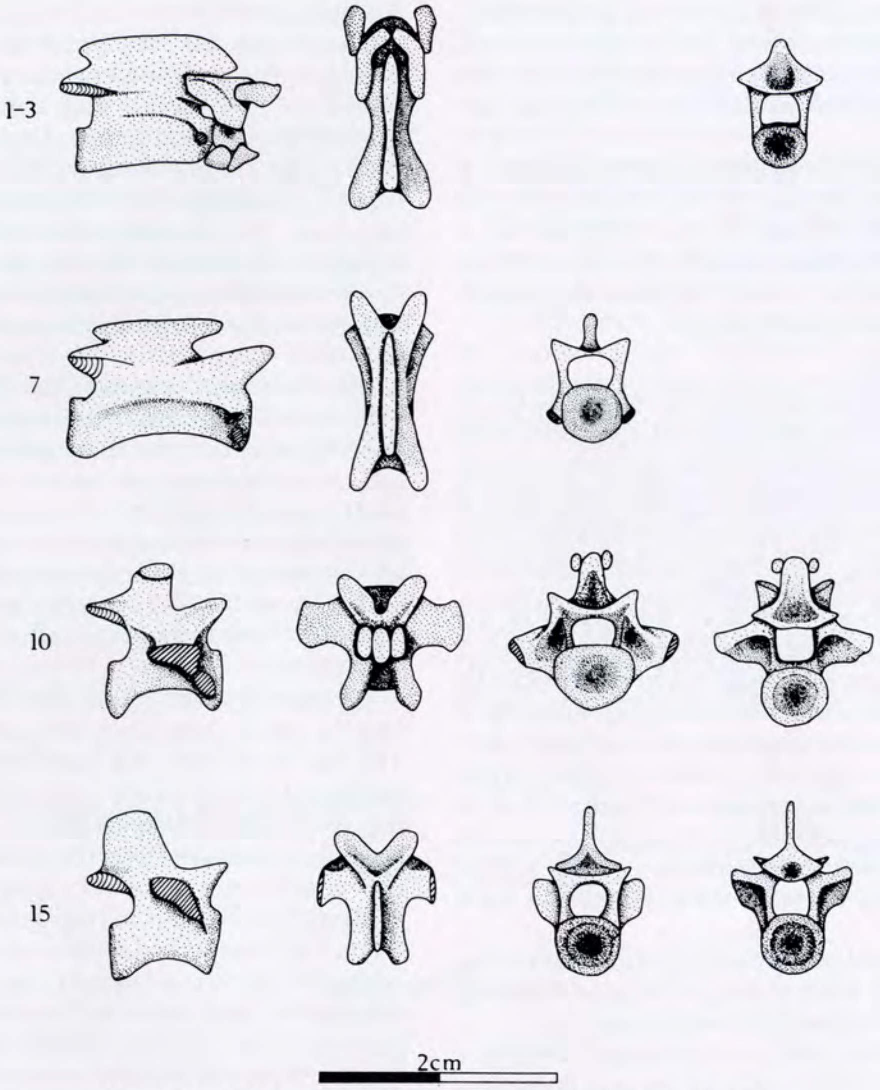


Figure 21. *Prolacerta broomi* B.P.I. 2675. Vertebrae as numbered.

posterior process contacts the ilium as he has shown.) The beginnings of a *Prolacerta*-like condition can be seen in *Youngina*, and several modern lizards trend the same way (Hoffsetter and Gasc, 1969, p.265).

*Caudals* (Figures 22 and 27). The string of 13 proximal caudals all have strong transverse processes diminishing gradually in size in the same way as do the neural spines and haemal arches. The chevron bones or haemal arches are laterally compressed and anteroposteriorly broadened: they are extremely long ($1\frac{1}{2}$ × the depth of the preceding vertebra). The enormously powerful tail indicated by the osteology almost certainly relates purely to the animal's bipedal mode of locomotion and active feeding movements of the head and neck, though the possible importance of lateral threat display cannot be overlooked.

*Ribs* (Figure 22). The cervical ribs have extremely slender shafts tapering to fine points; they have two distinct articular facets and an anterior dorsal process. Ribs 10 and 11 (in the pectoral region) are rather stout proximally; here the two rib heads have merged into a single articular facet. For the rest the ribs have slender shafts circular in section. From 19 to 26 the ribs are rather weak with expanded circular attachment facets, shafts very slender proximally, expanding a little distally.

*Pectoral girdle and forelimb* (Figures 23 and 30). The scapulocoracoid is extremely delicate, particularly that portion of the scapula anterior to the shaded line in the figure, which is paper thin. The posterior third of the suture between the two elements can be seen on the mesial surface. A coracoid foramen is present immediately in front of the screw-shaped glenoid.

Clavicles appear to elaborate with age (F is larger than G and therefore probably older, or possibly a male); unfortunately most of the medial shaft is missing. The vertical shaft is grooved on the inner surface where it would lie against the scapula. A prominent anteriorly directed boss appears to form with age in the angle between the two shafts.

The interclavicle is somewhat damaged though its essential structure is clear—it has a narrow medial shaft and a broad crosspiece notched anteriorly and with depressed facets on the ventral surface which receive the clavicles.

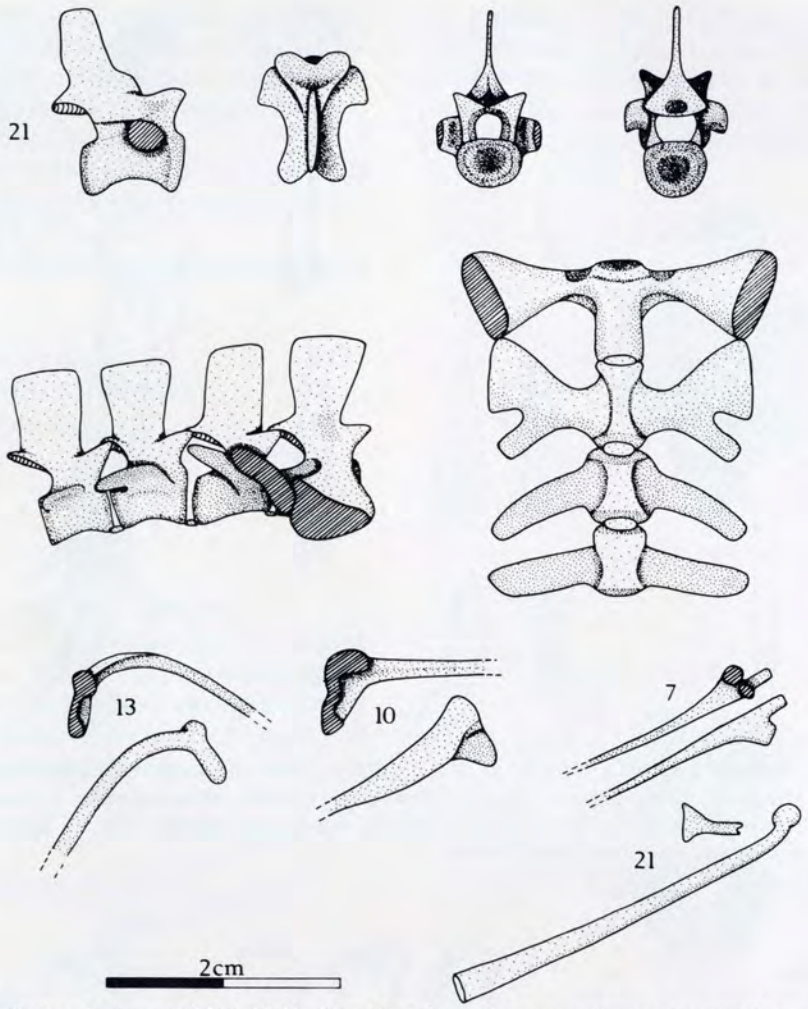


Figure 22. *Prolacerta broomi* B.P.I. 2675. 21st Vertebra; Sacrum and two proximal caudals in lateral and ventral aspect; Ribs as numbered.

The humerus is primitive and simple, though the entepicondylar foramen has been lost; there is a deep ectepicondylar groove.

Radius and ulna are long and slender. The small wrist elements preserved are as shown, but as they are somewhat disarticulated nothing definite can be said regarding the missing elements. The phalangeal count for the hand is the standard reptilian one.

*Pelvic girdle and hindlimb* (Figures 24, 31 and 33). All the elements of the pelvic girdle have smoothly rounded margins. All three contribute to the acetabulum which has no upper rim as such (though it is rimmed anteriorly by a ridge angled towards the posterior tip of the iliac blade)—this could be to allow the femur to be raised rather high during bipedal locomotion. The pubo-ischiadic plate is broad; the central area is extremely thin. There is a thickened out-turned anteroventral process of the pubis, with the obturator foramen immediately behind it. Girdle measurements relating to body sections are given in Table 1. p. 98.

The femur has marked posteriad curvature at the distal end. The head is concave and would thus have been capped by an epiphysis which would effectively increase the length of the femur. There is an internal trochanter, with intertrochanteric fossa, very much restricted to the head. The shaft is devoid of muscle attachment protruberances and scars. The tibia is large and robust, particularly at the proximal articulation; the distal end is concave and poorly ossified, suggesting the involvement of cartilage at this point. The fibula is rather slender and is laterally compressed.

The ankle comprises a proximal assemblage of astragalus and calcaneum in loose articulation with a large foramen between them, and a centrale in firm contact with the mesial surface of the astragalus. There are four distal elements of which the first three are small and featureless while the fourth is large with a lateral facet for the fifth metatarsal and a terminal facet for the fourth; it lies in the junction between astragalus and calcaneum.

There is a standard phalangeal count of 2:3:4: 5 : 4. The fifth metatarsal is hooked with a ventrolateral scar indicating the insertion of the gastrocnemius.

The astragalus has a large proximal facet which receives the tibia; this is followed by a smooth narrow neck before a second facet at right angles to the first.

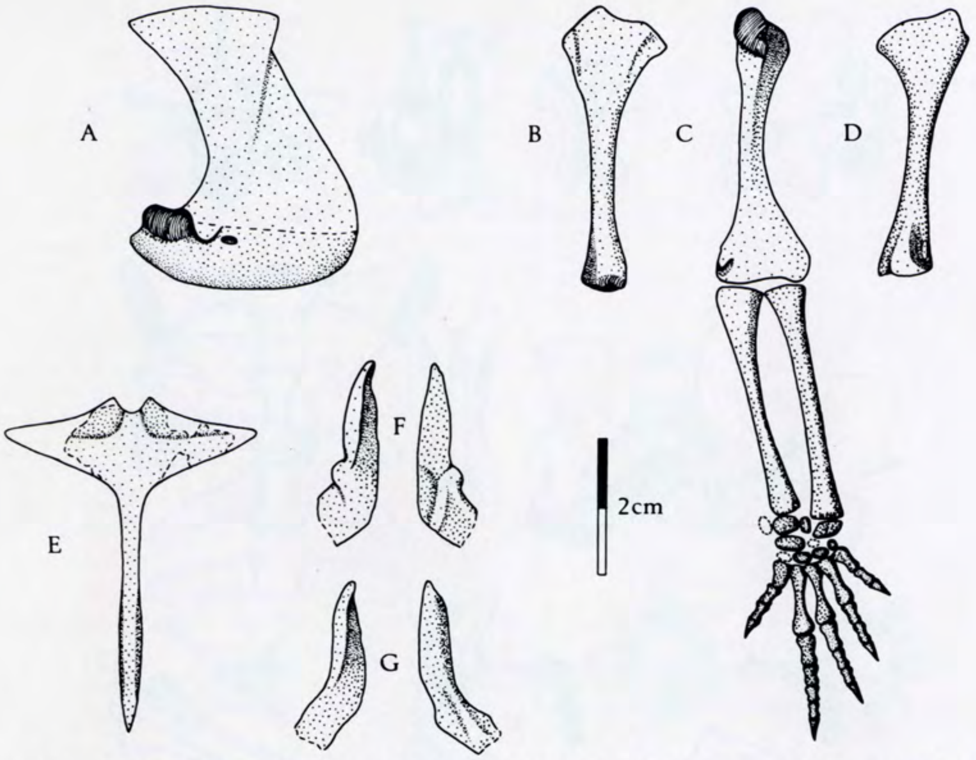


Figure 23. *Prolacerta broomi.* (A – E and G, B.P.I. 2675; F, B.P.I. 2676.) A, Scapulocoracoid; B, Humerus mesial view; C, Right forelimb; D, Humerus in lateral view; E, Interclavicle ventral view; F, Dorsal limb of clavicle, mesial and lateral views: G, Dorsal limb of clavicle, mesial and lateral views.

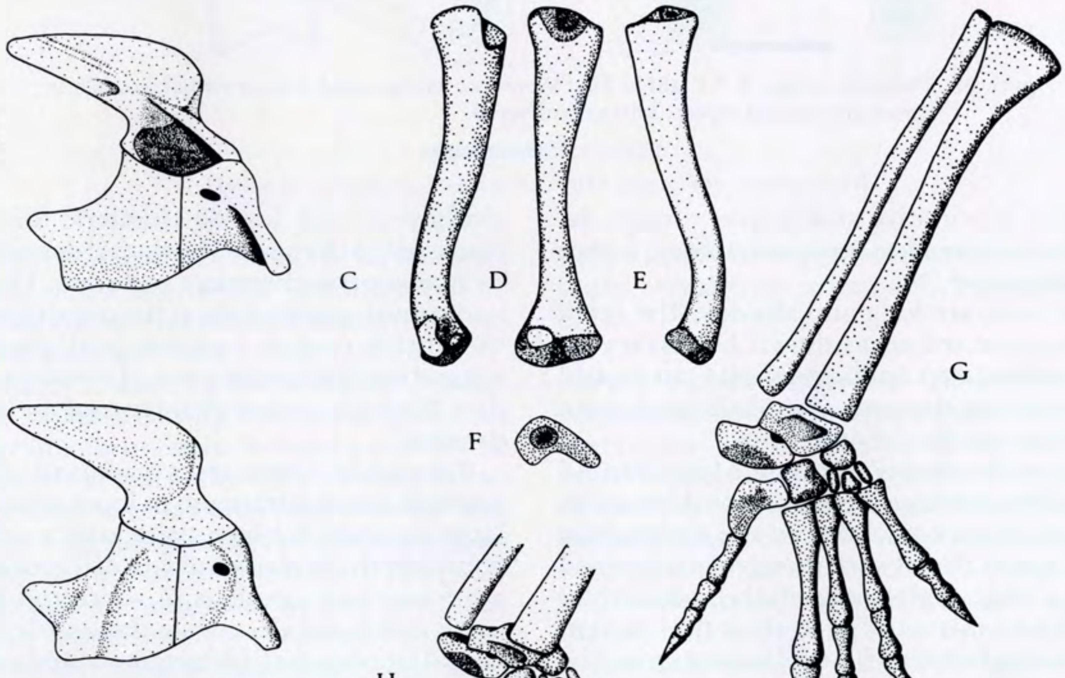


Figure 24. *Prolacerta broomi* B.P.I. 2676. A, Right pelvic girdle lateral aspect; B, Left pelvic girdle internal aspect; C – F, Left femur; C, lateral view; D, Posterior view; E, Mesial view; F, Proximal end; G, Right hind limb flat; H, Ankle flexed.

The calcaneum below this is of equivalent thickness, thinning a little from here towards its lateral edge. One can thus envisage a mass of cartilage here for reception of the fibula. The astragalus bears a marked depression in its dorsal surface as indicated.

Figure 24 G shows the hind-foot in one plane while in H a natural positioning has been attempted with the ankle flexed at the mesotarsal joint.

Some of the more important length measurements are as follows in mm:

| | |
|---|---|
| Skull (occipital condyle to snout) | 67 |
| Neck (condyle through ninth vertebra) | 100 |
| Trunk (glenoid to acetabulum) | 130 |
| Femur | 54 |
| Tibia | 58 |
| Humerus | 42 |
| Radius | 37 |

## *PROTEROSUCHUS* BRAINCASE

The braincase in B.P.I. 3993 (Figures 25, 26, 36 and 37) has suffered from the vertical compression which has affected the whole skull; no corrections have been made in the drawings except in Figure 26B which has been restored to symmetry.

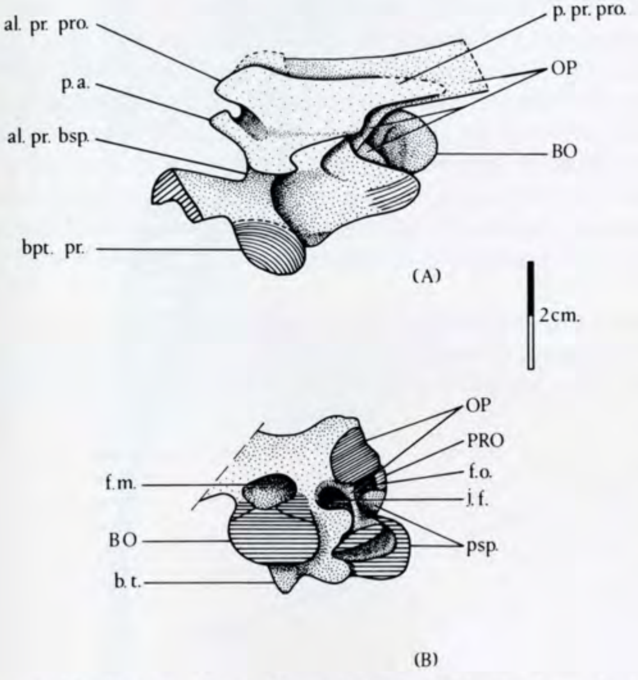


Figure 25. *Proterosuchus vanhoepeni* B.P.I. 3993, (Braincase); A, Lateral view; B, Somewhat oblique occipital view.

The *proötic* has an open trigeminal notch between well developed alar process and pila antotica: it has a long posterior process running along the paroccipital process of the opisthotic. A distinct ventral process meets the alar process of the basisphenoid; behind this a second process from the basisphenoid contacts the proötic. Anteriorly the proötics are united in the midline by a substantial sheet of bone, stretching from one pila antotica to the other, which roofs the pituitary fossa. This sheet is continuous with the dorsum sella; the exit for the VIth cranial nerve can be clearly seen (Figure 26A) between them. This condition also occurs in *Euparkeria*. The *basisphenoid* has several notable features. In lateral view (Figure 25A) can be seen the prominent process coming in behind the ventral process of the proötic; and thin bone behind it is folded inwards, as indicated also in Figure 25B. This arrangement floors the foramen ovale. The large postero-lateral processes of the basisphenoid bearing the grooves of muscle attachment scars run out beyond and below the ventral processes of the opisthotics—this is indicated in Figure 25B, a somewhat oblique view. In ventral aspect (Figure 26B) the basisphenoid runs anterior to and closely applied against the prominent basal tubera of the basioccipital, while just anterior to this is a deep depression. The open videan canals lie mesial to the posterior edge of the basipterygoid processes, while immediately in front of them are a pair of foramina (present also in *Prolacerta*) which possibly transmitted a branch of the palatine artery.

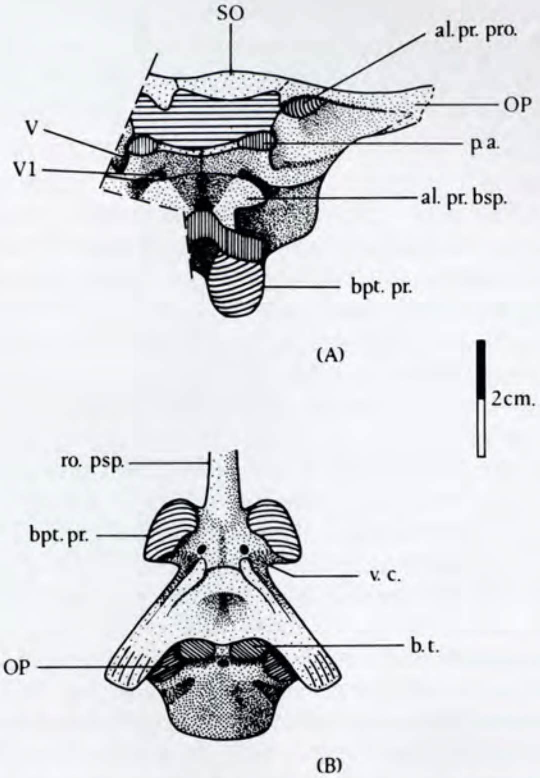


Figure 26. *Proterosuchus vanhoepeni* B.P.I. 3993, (Braincase); A, Anterior view; B, Ventral view.

The ear region poses a problem. The foramen ovale is very small. A stapes if present would have been restricted to a channel between opisthotic and proötic and would thus have run obliquely backwards to the head of the quadrate, indicating a tympanum in the position postulated by Ewer (1965) for *Euparkeria*. There is in any case no room for the attachment of a tympanum on the retro-articular process.

*Palatine*

Cruickshank (1972) shows the palatine forming the entire lateral margin of the suborbital fenestra. In fact it only runs halfway back. (B.P.I. 3993 and *P. fergusi.*)

*Streptostyly*

Cruickshank suggested that the quadrate of *Proterosuchus* might be movable. This is clearly not possible in an animal with a solid lower temporal bar. Variations in the position of the quadrate are apparently due solely to post-mortem distortion just as in *Youngina.*

## *PROLACTERTA* FUNCTION

(a) *Cranial kinesis.* It is well known that most if not all predatory squamates have kinetic skills. These are generally speaking small animals which swallow their prey whole. *Prolacerta,* though not a squamate, is functionally similar. A small, lightly built predator, it is the epitome of the sort of animal to which cranial kinesis is of advantage. In *Prolacerta* the skull can move in a vertical plane relative to the braincase, pivoting on the paroccipital processes, the palate being guided by the basal articulations of the basisphenoid. The quadrate is free to move anteroposteriorly as a result of the loss of the lower temporal bar; this is the only acceptable explanation for the retention of the quadratojugal as a delicate strut articulating between squamosal and quadrate. (One can readily accept that slight refinement to the quadrate controlling mechanism in a more advanced form would render the quadratojugal superfluous, but there is no reason to believe that this type of quadratojugal mechanism formed part of the lizard evolutionary story.)

Certain less obvious movements are also possible. These involve the jugal and postorbital, and may be connected with either streptostyly (fore and aft movements or quadrate spreading) or muzzle movements, or both.

Some lateral movement of the postorbital along its vertical contact with the postfrontal would have been possible though slight. The postorbital/squamosal contact is loose and would allow free movement in anteroposterior and dorsoventral planes. The tongue and groove contact between postorbital and jugal would allow sliding movement, and it seems logical to assume a fair degree of the same sort of sliding at the long curving jugal-maxillary junction. The great reduction of jugal and postorbital in recent lizards and the loss of contact between them, as for example in *Varanus,* would suggest that jugal/postorbital sliding is necessary in the early stages of the development of mesokinesis. Movements at the upper extremities of the postorbital in *Prolacerta* might be related more to quadrate movements. Although there is no mesokinetic joint as such, yet the bones of the snout are extremely thin and the fenestrae exochoanis very long, so that muzzle flexure by actual bending of particularly the nasals almost certainly occurred.

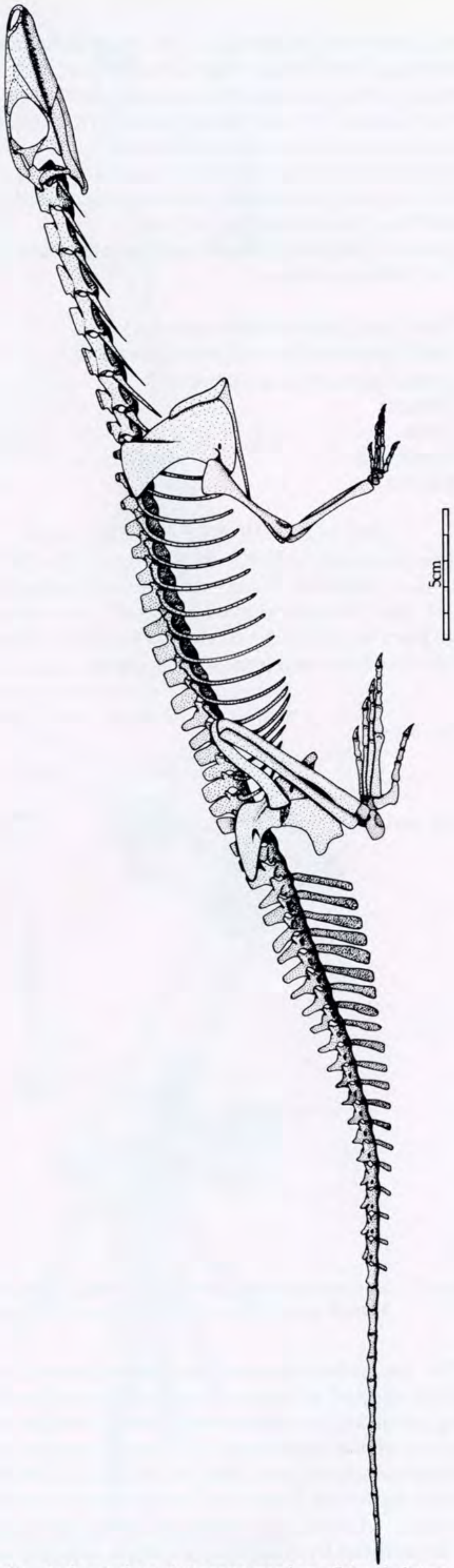
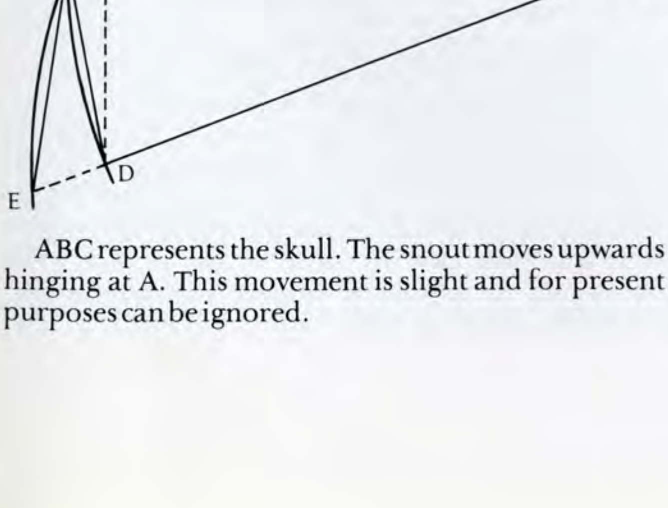


Figure 27. *Prolacerta broomi,* Reconstruction of the skeleton.

It is interesting to note the movable joints present in lizard skulls (Frazzetta, 1962) which are not present in *Prolacerta*. In all lizards which have a mesokinetic (fronto-parietal) joint, the skull roof is broadest at the straight transverse fronto-parietal suture. In millerosaurs, younginids and *Prolacerta* this marked broadening is lacking and the fronto-parietal suture is W-shaped, effectively preventing flexure at this point. In this context the keuhneosaurs are intermediate in morphology, though apparently not yet mesokinetic (Robinson, 1966). Associated with mesokinesis in lizards is antero-posterior movement of the pterygoids. This is reflected in a sliding basal articulation and a rod-like epipterygoid which pivots at both ends. In *Prolacerta* there is no suggestion that the basal articulation is moving in this direction and the epipterygoid has an antero-posteriorly elongated footplate which could not conceivably have pivoted. Relative movement between pterygoid and quadrate certainly occurred.

Slight spreading of the pterygoids and hence of the quadrates and lower jaw rami is a possibility, but until both the movements and their functional importance can be convincingly demonstrated in living lizards, there is no purpose served by discussion at this stage. Frazzetta (op. cit.) has shown that the lizard quadrate moves forward as the jaws open; it would thus be reasonable to assume that the same is true of *Prolacerta*. Now while kinesis in *Prolacerta* is not as complex as that described by Frazzetta for lizards, there appears to be a very simple explanation for quadrate protrusion. Upward movement of the skull on the braincase as the jaws open is slight, and any upward movement of the whole head will not alter the fact that the lower jaws are dropped through a considerable arc relative to the upper.

This means that without protrusion of the quadrate the lower teeth move posteriad relative to the upper, and consequently move forward during the bite, as shown in the following diagram.



ABC represents the skull. The snout moves upwards hinging at A. This movement is slight and for present purposes can be ignored.

BD represents the lower jaw, hinging at B.

CF represents the extent of posteriad movement of lower teeth relative to upper in an akinetic skull.

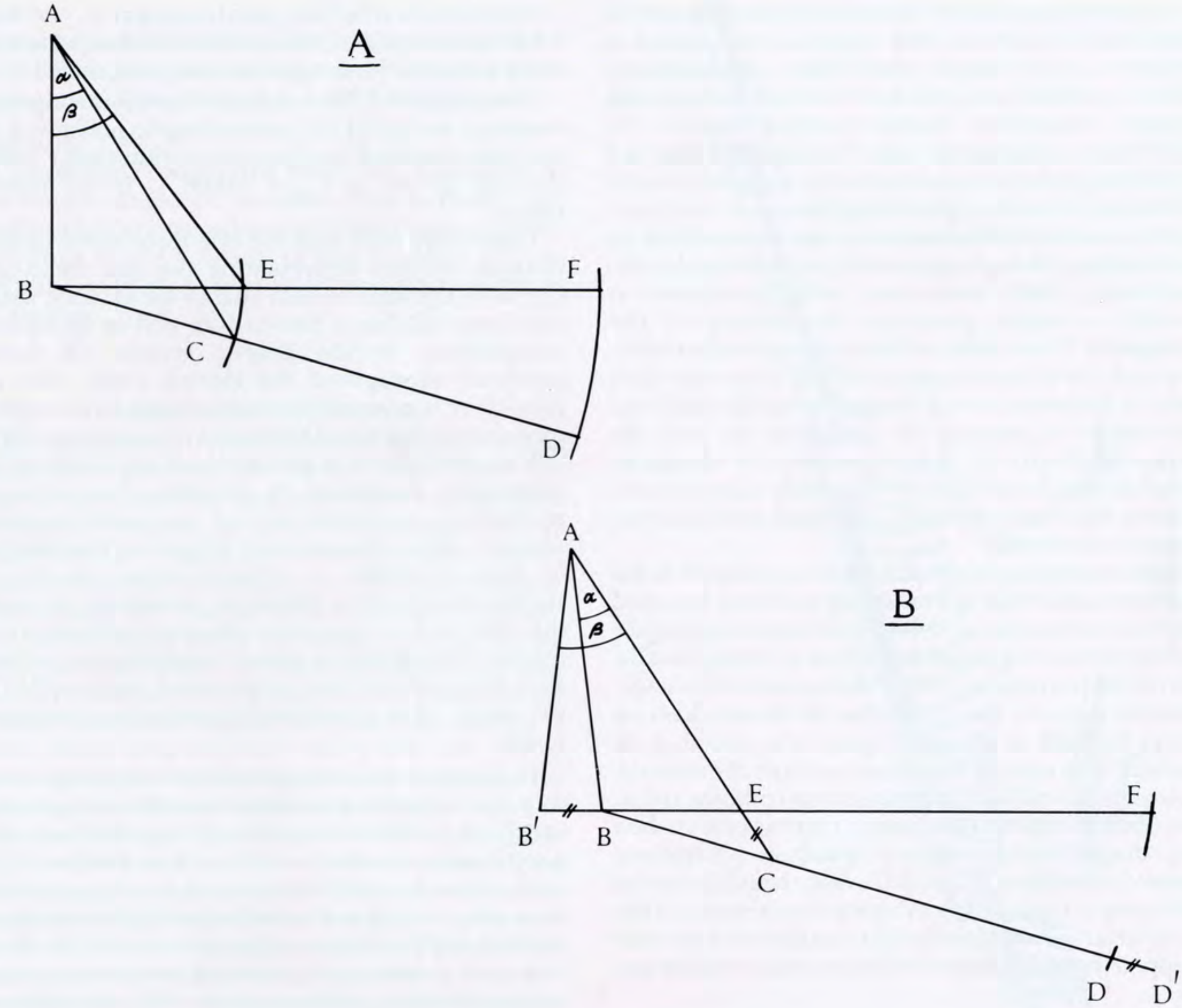
Protraction of the quadrate during jaw opening results in the tip of the jaw moving to position E. As the jaws close and the quadrate is retracted E moves through an arc to C, as would D in an akinetic system.

Clearly the teeth and the bite force move upward through an arc. Representing the bite force as a chord on this arc it is clear that in the akinetic system this force CD has a forward as well as an upward component. In the kinetic system CE moves posteriad throughout the closing cycle. This circumstance is governed by two variables, the angle of the jaw opening θ and the extent of protrusion DE.

θ as used above is greater than any angle of jaw depression illustrated by Frazzetta, but it is still necessary to determine DE for live lizards to decide whether natural movements fall within the limits set by these variables. It certainly seems plausible to suggest that there could be an advantage in having the teeth and the bite force directed backwards during jaw closing for an animal capturing active prey. It is surely more than coincidental too that ECD is the shape of a generalised carnivorous thecodont tooth.

Compare the akinetic system (A) with the kinetic system (B) p. 114. In both the muscles contract from length AC to length AE. In both $\alpha$ decreases to $\beta$. But, whereas in A the direction of pull shifts from AC to AE, in B AE and AC lie on the same line, with C moving to E as B moves to $B^1$. Note that in B quadrate retraction B B′ = adductor shortening CE = degree of jaw protrusion D D′. As any biological system can be expected to represent a compromise between conflicting ideals, B B′ is probably too short to allow perfection of system B though the system yet holds considerable advantage by virtue of the extra linkage and more nearly constant line of action of the adductors.

Streptostyly seems to hold an irresistible fascination which has led to some curious statements in the literature. Some of these merit brief consideration. Walker (1961) suggested that the quadrate of *Stagonolepis* (a pseudosuchian) might have been movable and have played a part in that animal's shovel-snouted foraging mechanism. Ewer (1965) suggested that some movement of the quadrate may have been possible in *Euparkeria*, a thecodont, and suggested the presence of an additional wholly unnecessary and improbable protractor muscle attaching to the mesial surface of the quadrate ramus of the pterygoid, i.e. that portion which lines the throat. Cruickshank (1972) has suggested that the *Proterosuchus* quadrate may have been movable—this to account for the variability in the slope of the quadrate exhibited by several skulls. The fact remains that *Proterosuchus* has a solid lower temporal bar and the quadrate always bears the same relationship to it; it



therefore seems more reasonable to attribute this variability to distortion of the specimens. It would be unexpected to find a streptostylic quadrate in any diapsid, as meaningful movement is only possible once the lower temporal arcade has been breached as in *Prolacerta*.

There is merit in Robinson's (1966) suggestion that the quadrate (of lizards) might rock back and forth during chewing movements thus aiding swallowing. Whether this is true of any lizards will require experimental determination. In particular it is necessary to determine what sequence of muscle actions is responsible for quadrate retraction and to what extent these movements are independent of jaw adduction.

(b) *The postcranial skeleton.* It is no exaggeration to say that the combination of characters which make up the skeleton of *Prolacerta* (and *Macrocnemus*) is unique.

This is a small, very light-boned animal, unquestionably built for speed and/or agility. Limb disparity *per se* is a vague and misleading term. What is important as a clue as to whether an animal was terrestrial quadrupedal, aquatic or bipedal, is the relative lengths of femur and tibia: in a terrestrial quadruped these are subequal in length, in aquatic animals the tibia is markedly shorter and in bipedal animals the tibia is the longer bone. Hence we can say that *Prolacerta*, on the basis of limb proportion, was bipedal (at least at speed). This, however, is the only immediately apparent indicator of bipedality; there is no indication, particularly in the pelvic girdle, of supporting modifications for this mode of locomotion.

Looking for comparisons then we can look first at the lizards. Several lizards are known to adopt a bipedal stance and/or gait at times. This subject has been well covered in a delightful chapter by Neill (1971), whose main thesis it is that bipedality arose in arboreal lizards as a predator confrontation and escape mechanism and is only employed by them as such. The bipedal lizards are characterized by long slender tails which are important in counterbalancing the weight of the head and trunk during this rather ungainly gait (described by Snyder, 1949, 1954, 1962). One aspect of this crude bipedal gait which has seemingly escaped notice is the rotation which occurs at the foot in contact with the ground as the opposite limb is swung forward in stiff-legged fashion: this can easily be seen in the scratch marks of the toe impressions left by a basilisc chased across a damp clay surface. This is worth recording for the implications it may have for ankle structure, though *Prolacerta* itself has a typical early thecodont ankle and it is remarkable that very little osteological modification, limb disparity excepted, is seen in the early stages of bipedalism.

A disconcerting aspect of bipedal lizard morphology from the point of view of this discussion is that they all have short necks and trunks; however, we can immediately remark that perhaps the deep rooted tail of *Prolacerta* is designed in part to counteract the added weight of the long neck. There are at least two other factors to consider here.

Leaving the lizards for the moment it is pertinent at this stage to introduce another tentative comparison. Both the long neck and the large flattened chevrons of *Prolacerta* invite comparison with the incipiently bipedal prosauropod dinosaurs.

We are now at the stage where we can embark on detailed argument on the function of the *Prolacerta* skeleton. To start with the tail. The bipedal lizards have long slender tails with rather insignificant chevrons; one aspect of the function of this tail has been overlooked. While it is clear from Snyder's (op. cit.) drawings and photographs that the distal part of the tail is flung out to counterbalance the body, it is equally clear that the base of the tail is held in line with the pelvis and both it and the trunk are thrown over to the same side as the limb executing the powerstroke. This probably ensures that the direction of pull of the femoral retractors places the arc of travel of the femur in the required plane, and it also helps distribute the necessary weight over the sacral region (weight against which the limb is pushing). As far as the use of the tail as a counterbalance to the weight of the body is concerned this is something which requires further explanation as we are dealing with a state of dynamic equilibrium in which weight distribution clearly changes considerably through the stride sequence.

The above remarks serve to highlight the importance of the second sacral rib of *Prolacerta* doubling as a caudal transverse process tending to lock the base of the tail to the sacral region; this also suggests a reason for the impression of relative rigidity conveyed by the *Prolacerta* chevrons (one may note by way of contrast that in the varanids which use their tails as lashes the chevrons are centrally situated on the centra, thus not impeding flexure in any way).

The caudal chevrons of *Prolacerta*, in proportion, must be among the largest on record. At the base of the tail they are 1,5 times as long as the depth of the preceding vertebra and this ratio gradually decreases to unity. The only acceptable explanation for this is that of concentrating the bulk of the muscle mass ventrally at the proximal end of the tail. There is almost certainly more than a simple weight factor involved here; as the pelvis shows no evidence of improvement of the locomotor musculature for bipedal locomotion it is quite likely that the main femoral retractor, the *caudifemoralis longus*, would be considerably enlarged in an animal of this size (the size limit of bipedal lizards). Femur morphology shows that the caudifemoralis inserted near its proximal end, an arrangement which sacrifices power for speed.

The shape of caudal chevrons in reptiles is rather variable; as this is an aspect largely ignored one can find little help in the literature, but comparison with the incipiently bipedal dinosaurs is striking, in that the chevrons are rather large and laterally compressed: while these prosauropods have long necks, there is not much skull weight to counterbalance, and in any case one cannot compare locomotion in early thecodonts and dinosaurs too closely. It is instructive to note, however, that in *Saltoposuchus*, a bipedal dinosaur with large head and carnivorous dentition, the cervical vertebrae are extremely short.

A deep tail must inevitably raise the possibility of its being an adaptation to swimming. Fortunately that possibility is easy to discount in this case. In the crocodile which is adapted to an aquatic existence the chevrons are of more moderate size, narrow, and circular in section; the tail is dorso-ventrally symmetrical with tall neural spines extending almost to the tip. In *Prolacerta* the neural spines become insignificant in the distal half of the tail. In the extinct marine reptiles caudal chevrons become very small and insignificant. A piece of circumstantial evidence against an aquatic existence is worth mention. *Macrocnemus* occurs in association with a highly adapted aquatic fauna which tends to underpin the non-aquatic nature of *Macrocnemus*.

The long neck of *Prolacerta* may account in part for the extra weight at the root of the tail. The long neck is a typically thecodont specialisation common to Proterosuchians, certain dinosaurs and birds. This is a specialisation which considerably enhances the predatory capability of the animal. The thickened neural spines at the base of the neck and in the pectoral region are sites of attachment for powerful, quick-acting muscles concerned with raising the head and neck and with lateral movements.

With regard to the limbs and girdles the latter are extraordinarily primitive for such an advanced animal, conveying no hint of the animal's obviously rapid, often bipedal, gait. Though the hind limb is long with tibia longer than femur, yet it shares a primitive ankle pattern with *Proterosuchus* and rhynchocephalians. The hammate process of the fifth metatarsal shows no sign of turning inwards underneath as is the case in bipedal lizards (Snyder, 1954). The forelimb is not reduced and probably functioned during slow locomotion, basking (Figure 27) and tree climbing.

## ECOLOGY

### *Possible environment and habits*

The *Lystrosaurus* zone presents many problems of interpretation of ecology of its fauna. A regional sedimentological study is an essential prerequisite as a framework in which to place the fauna, but this is as yet lacking. This is a zone notable for its omissions; there is, for instance, little evidence of vegetation. Another notable omission is the total absence of fish to date, though these must have been present in an environment which supported labyrinthodonts. Of the many invertebrates, including insects which must have been present, only millipedes have so far been recorded.

Considering its early thecodont ancestry it is possible that sharp blade-like teeth were the only option available to *Prolacerta*; these are small in relation to the size of the skull, compared with the teeth of, for example, *Euparkeria*. (This applies as well to *Proterosuchus*.) Unfortunately no living reptiles have comparable dentitions with the possible exception of *Varanus komodoensis*. *Prolacerta* might be envisaged as feeding on small prey which it would grab, kill, and swallow whole, such as the young of the many small synapsids, procolophonids and labyrinthodonts known from the *Lystrosaurus* zone, as well as insects. It seems very likely that the prolacertids were replaced by true (pleurodont) lizards.

The rather larger *Proterosuchus* on the other hand probably fed by tearing pieces of meat off a carcass much as does *Varanus komodoensis*, as the teeth of these two animals are closely comparable in size relative to the skull, in shape, and in having finely serrated posterior edges. *Prolacerta* lacks serrations on the teeth and as these are present in *Heleosaurus* and *Proterosuchus* they have presumably been secondarily lost in *Prolacerta*.

Stealth more than agility would be required in hunting. Why then this light, swift creature? Presumably no contemporaries could match *Prolacerta* for speed, though some Galesaurids and Therocephalians would certainly have eaten them, given a chance. The most likely explanation is that it was to an extent arboreal—here lightness and agility are of advantage. This would support Neill's (op. cit.) argument for a close link between an arboreal existence and the evolution of bipedality (in animals of this size).

## RELATIONSHIPS OF *PROLACERTA*

Comparisons of all the possibly significant features of *Prolacerta* cover a very wide field indeed. Some of them are rapidly discountable, most flounder on inadequate knowledge of many forms, but in the end the reasonable options are few and a stable picture seems to emerge.

Some of the earlier Permian diapsids should be mentioned. *Petrolacosaurus* is a Pennsylvanian form technically diapsid but remote in time and lacking the strong morphological features which link the late Permian and Triassic forms. *Areoscelis* merits attention as the only fairly well known protorosaurian. Relationship to *Prolacerta* has been argued by Camp (1945), Romer (1947) and Vaughn (1955). The only striking parallel is in the elongation of the cervical vertebrae, but this feature is common to several unrelated groups. *Areoscelis* has in fact a curious specialised postcranial skeleton (e.g. the elongate limbs) behind a primitive skull—certainly not a good generalised ancestor. The double coracoid is another point against it.

One animal which must be revived in this discussion is the Russian Permian *Mesenosaurus*. Here is an animal with powerful carnivorous dentition (mode of implantation unknown), a lower temporal opening with lower temporal bar, several primitive characters such as the maxilla entering the external naris, which should merit consideration with early thecodonts, but about which too little is known.

An early Permian diapsid is *Mesosaurus*, a curious, little known, highly specialised form, but which with *Petrolacosaurus* stands as a caution that diapsid sauropsids became established early on. Hopefully, the Brazilian material, reputedly of excellent potential, will yield a good account of this animal.

One arrives then at the Eosuchia, the millerosaurs, younginids, rhynchocephalians (sphenodontids), squamates and archosaurs (Thecodontia) for present purposes, and the problem of relationships of these groups.

The millerosaurs, which may or may not have direct bearing on later phylogenies, nevertheless exhibit certain morphological details which are not shown by, for instance, the younginids but which go a long way to explain the derivation of early thecodont characters (particularly one may mention the quadratojugal and its relationships).

Among the younginids, *Youngina* as described above gives an apparently satisfactory rhynchocephalian ancestor, but it is necessary to note here that all the known rhynchocephalians have basically crushing dentitions and virtually akinetic skulls.

*Heleosaurus* (to be described by Carroll) is a good thecodont ancestor with its blade-like marginal dentition and advanced femur indicating bipedality.

Much use has been made here of the term "thecodont" as *Prolacerta* is so obviously a thecodont while the squamates are typically acrodont or more commonly pleurodont (Edmund, 1969). This applies to the earliest recognised true lizards, the keuneosaurids, which are defined as having subpleurodont teeth.

*Paliguana*, contemporaneous with *Prolacerta*, is a poor specimen, yet it has very much the morphology and proportions of the keuneosaurids. One or two probable lizard skeletons are known from the Permian of South Africa, of which *Palaeagama* (Broom, 1926) has been described; unfortunately the temporal region is badly damaged. Carroll believes he can reconstruct it to look much like the keuneosaurids.

The lizard-like animals mentioned in this paragraph are to be described by Carroll. There is thus some evidence to suggest that the Squamata had evolved before the end of the Permian, though more collecting is needed to strengthen this.

To place *Prolacerta* then we are left with two options. Detailed comparisons with primitive thecodonts prove instructive, as do comparisons to the Protorosauria (sensu Romer, 1956). Comparisons between *Prolacerta* and *Macrocnemus* are so close there can be little doubt of a close relationship. Other Protorosaurs are so poorly known that they cannot be drawn into this relationship with certainty.

*Proterosuchus* (Cruickshank, 1972) is the one animal close to *Prolacerta* known in sufficient detail for meaningful comparison. Much of the material has also been available to the writer when additional information was required. *Proterosuchus* occurs consistently lower in the *Lystrosaurus* zone than does *Prolacerta*, but this probably does no more than reflect an ecological separation. *Proterosuchus* is a larger, more heavily built, and quadrupedal animal, while *Prolacerta* is small, light and bipedal. *Proterosuchus* has an antorbital fenestra which puts it among the Archosauria, but Cruickshank has suggested with some justification the derivation of *Proterosuchus* from a "rhynchocephalian" ancestor; such an animal would be required not to possess an antorbital fenestra, and this step would not have been far back in time.

Strip *Proterosuchus* of its archosaurian label and compare with *Prolacerta*. The skull morphology and detailed relationships of the bones are remarkably close. The writer does not accept Cruickshank's interparietal, nor the jugal process of the quadratojugal which he shows. The palatine does not form the entire lateral margin of the suborbital vacuity as he shows, but only runs halfway back. Cruickshank failed to note that the teeth of *Proterosuchus* are serrated on their posterior margins.

Having disposed of these points the differences are now only of degree and quite consistent with the basic differences of size and build.

*Proterosuchus* has apparently a proportionately longer snout, achieved by compressing the orbit, with a more downturned premaxilla; it has a very odd retroarticular process (for which a functional interpretation is required). It is difficult to accept Cruickshank's assertion that the quadrate was streptostylic. Surely this can only occur once the lower temporal bar has been breached?

The postcranial skeletons of the two animals present a very similar morphological grade. The girdles of *Proterosuchus* are heavier, interclavicle and ilium having distinctive shapes. The bifurcations of the sacral processes were one of the first points of strong similarity noted in this study.

Similarity extends to the hind foot and ankle, though there is some doubt regarding the phalangeal count of *Proterosuchus*. Cruickshank has called the astragalus intermedium when it is really a compounding of intermedium and tibiale, and the centrale he calls astragalus. Names aside, the feet of *Prolacerta* and *Proterosuchus* are identical down to the hooked fifth metatarsal.

The vertebral columns are very similar, though *Proterosuchus* does not have such elongate cervicals. This similarity extends to the large blade-like caudal chevrons, though these are only two-thirds the length in *Proterosuchus*.

All the above gave sufficient grounds for expecting to find an explanation for the braincase of *Prolacerta* in *Proterosuchus*. One may expect braincases to be fairly conservative at this level; also, while that of *Prolacerta* is poorly ossified in places, this is consistent with a light kinetic skull, while in the larger *Proterosuchus* the braincase is well ossified. This comparison, detailed elsewhere, is so striking in every detail as to put the seal on a very close relationship.

The quadratojugal may be one of the more important elements in deciding lizard/rhynchocephalian/archosaurian relationships. Gow (1972) has described the relationships of this bone in millerosaurs in detail, and this pattern could very easily give rise to what we see in *Prolacerta* and *Proterosuchus* and the later archosaurs, e.g. *Euparkeria* (Ewer, 1965) where the quadratojugal rests on a facet on the lateral condyle of the quadrate running up to meet the squamosal above, lateral to a quadrate foramen. From the reduced condition in *Prolacerta* it is of little consequence whether this bone is lost or retained by *Macrocnemus*. It is difficult to see how this quadratojugal arrangement could be derived from *Youngina*.

The Triassic reptiles of Monte San Giorgio (Kuhn-Schnyder, 1963 and others) are a diverse collection mostly of specialised marine forms; it is thus surprising to find amongst them an animal very close indeed to *Prolacerta*, namely *Macrocnemus bassanii* Nopsca. Owing to their poor mode of occurrence these fossils are not as well known as one would like, particularly in details of skull structure. Nonetheless Kuhn-Schnyder (1963) described a skull of *Macrocnemus* in sufficient detail to conclude convincingly that this animal is closely allied to *Prolacerta*. In that paper he suggested the possibility that the lower temporal opening of diapsids evolved before the upper. The writer has suggested (Gow, 1972) this might apply in the origin of squamates. In view of the standard morphology of upper temporal openings of younginids and early thecodonts and bearing in mind the presence of two temporal openings in the upper Carboniferous *Petrolacosaurus* these suggestions are open to doubt. It seems likely that the lower temporal bar has been lost (along with the quadratojugal?) in *Macrocnemus* and *Tanystropheus*. *Prolacerta* constitutes the ideal starting point for the derivation of these forms.

In Kuhn-Schnyder's 1963 paper there is an excellent photograph of an almost complete skeleton of *Macrocnemus*. The resemblance to *Prolacerta* is so close as hardly to bear detailing and should dispel all doubt regarding the close relationship of these animals. Further checks against Peyer's (1937) original detailed description of *Macrocnemus* with its many excellent photographs also serve as a good standard of comparison.

Size, proportion and morphology are closely comparable in the two animals. The few concrete differences are predictable and only slight advances occur in *Macrocnemus*.

As far as the *Macrocnemus* skull is known it is very similar to that of *Prolacerta*. Doubt exists as to the nature of the snout and the position of the external nares. The hind margin of the jugal is not known with certainty, nor can the presence of a quadratojugal be shown, though it seems certain that no lower temporal bar was present. Details of squamosal, quadrate and upper temporal fenestra are identical to the condition in *Prolacerta*. Dentitions are very similar in the two animals. What can be seen of the palate of *Macrocnemus* agrees well, and the shape of the basisphenoid is identical.

The vertebrae and ribs agree very closely, even to the divided second sacral transverse process and the large flattened caudal chevrons.

Ossification of the girdles in *Macrocnemus* shows a considerable reduction over that in *Prolacerta* but this is almost universal in middle Triassic reptiles and to be expected and involves just those areas that are extremely thin in the girdles of *Prolacerta*. The ilium and inter-clavicle are still virtually interchangeable between the two animals. Limb proportions are the same in both animals, both have hooked fifth metatarsals and the same digital formulae. Slight differences in ankle morphology reflect only the time gap.

It is thus clear that *Prolacerta* is representative of an as yet poorly known group of early Triassic prearchosaurian thecodonts which in all probability gave rise to the later *Macrocnemus* and *Tanystropheus*. These can then be regarded as a sterile group which paralleled the Squamata in the loss of the lower temporal arcade.

## *PROLACERTA*—SYNONYMY AND DIAGNOSIS

Subclass: Incertae sedis

Probably most workers would favour retention in the Lepidosauria

Order **Parathecodontia** nov.

Thecodont reptiles of diapsid origin in which the lower temporal arcade has been breached. Very closely allied to proterosuchian thecodonts in most aspects of skeletal morphology but precluded from the Subclass Archosauria by the almost certainly primitive absence of antorbital fenestrae.

Family Prolacertidae Parrington 1935.

Small agile light-boned bipedal animals. Quadrate streptostylic and quadratojugal reduced or absent.

*Prolacerta broomi* Parrington 1935.

= *Pricea longiceps* Broom and Robinson, 1948.

Lower Triassic prolacertids from the *Lystrosaurus* zone of South Africa. Girdles large, unfenestrated, plate-like structures. Jugal spur and quadratojugal present.

*Macrocnemus bassanii* Nopcsa 1930

European Middle Triassic prolacertids. Girdles reduced. Posterior border of jugal smooth, quadratojugal absent.

Family Tanystropheidae Romer 1956.

*Tanystropheus longobardicus* Meyer 1852.

Skull very similar to that of Prolacertidae but with heterodonty in juveniles, in which the teeth in the posterior half of both jaws are tricuspid. Greatly elongate neck with longest neck vertebra five times as long as the longest trunk vertebra. Considerably larger than Prolacertidae—in excess of four metres in length.

## DISCUSSION

*The reptilian braincase*

Although it is now known that the incomplete lower temporal bar is not confined to lizards but is present also in the sphenodontid *Glevosaurus* (Robinson, 1973) and certain millerettids (Gow, 1972), and in spite of the fact that *Prolacerta* has blade-like carnivorous theodont dentition, it seems desirable to establish the differences between squamates and archosaurs on as many features as possible, particularly those of a predictably conservative nature. Clear differences in braincase morphology would provide this additional distinction. Here good comparative information is scarce, particularly as regards good illustrations, but this situation is starting to change and new work on reptilian braincases can be expected to appear in the near future. There is enough material available for certain trends to be discernible and putting these forward at this stage may provide guidelines and ideas for future work.

A problem is that several strong features of typical lizard braincases tend to lose significance the farther one goes back in time, and in any case squamate history below the upper Triassic is vague at the least. To illustrate the point, take the foramen rotundum found in lizards; this is lacking in *Youngina*, millerettids and *Sphenodon*; it is lacking in archosaurs, some of which develop a foramen pseudo-rotundum. Apparently the Kuehneosaur braincase is still Permian in this respect (Robinson, 1973).

The ventral process of the opisthotic thought by Robinson (1967) to be a unique character linking *Prolacerta* and *Kuehneosaurus* is in fact typical of the lower Triassic proterosuchians and were it not for the fusion of opisthotic and exoccipitals in later forms it might be possible to extend this to modern lizards and the sauropod dinosaurs at least.

However, the negation of the usefulness of the above points notwithstanding, there does seem to be a concrete basis for separation on braincase features. The millerettid-younginid grade braincase could lead anywhere, but approaching the problem from the other end a clear difference between lizard and archosaur is in the extent of participation of the parasphenoid (basisphenoid when the two are no longer distinguishable) in the sidewall of the braincase. In *Prolacerta, Proterosuchus, Euparkeria* and *Stagonolepis* this is extensive, while in lizards the braincase is walled completely by proötic and the basisphenoid terminates abruptly much farther forward (e.g. *Varanus*, Figure 28). On this basis it seems there can be no ambiguity regarding the correct assignment of Triassic fossils, though it appears at this stage that the archosaurian condition became firmly established earlier than that of lizards.

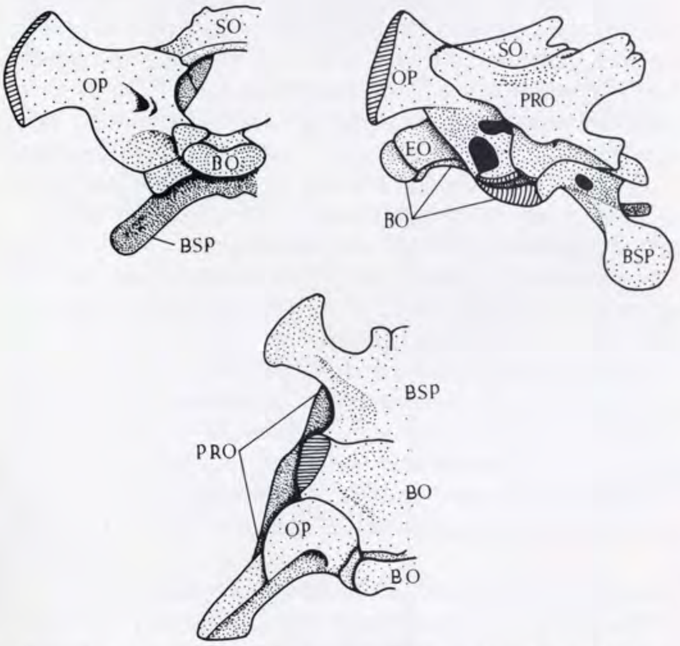


Figure 28. *Varanus*, Braincase in occipital, lateral and ventral views. Note particularly the restricted extent of the basisphenoid, both laterally and posteriorly.

The above suggestions are now considered in greater detail.

At the level of *Youngina* and *Milleretta* the braincase is essentially captorhinid (*Milleretta* has an odd stapes while that of *Youngina* is more like the slender rod seen in later reptiles, but this does not affect braincase morphology). Perhaps the braincase in these animals could be said to represent an upper Permian level of development, just prior to considerable changes taking place, but it is necessary to bridge the middle Permian gap in the reptile story before this can be stated with certainty. A feature of this braincase is the nature of the parasphenoid. Gow (op. cit., Figure 9C and p. 239) was able to demonstrate that the parasphenoid in millerettids runs right back beneath the basioccipital almost to the condyle. The basisphenoid, comprising the basipterygoid processess, sella turcica and dorsum sellae lies on top of the parasphenoid, while between basisphenoid and basioccipital is an extensive gap bridged only by parasphenoid. An exactly similar condition is indicated for *Youngina* (Figure 5C). The millerettid parasphenoid is characterized by a toothed rostrum plus two teeth on either side of the base of the rostral row; this is very similar to the condition in *Petrolacosaurus* (Figure 30). In *Icarosaurus* (Colbert, 1970) and *Kuehneosaurus* (privileged data from P. L. Robinson) these parasphenoid teeth are retained. In recent lizards, typified by *Varanus* (Figure 30), the parasphenoid seems to be reduced to the cartilaginous rostrum, leaving only basisphenoid flooring the braincase anteriorly.

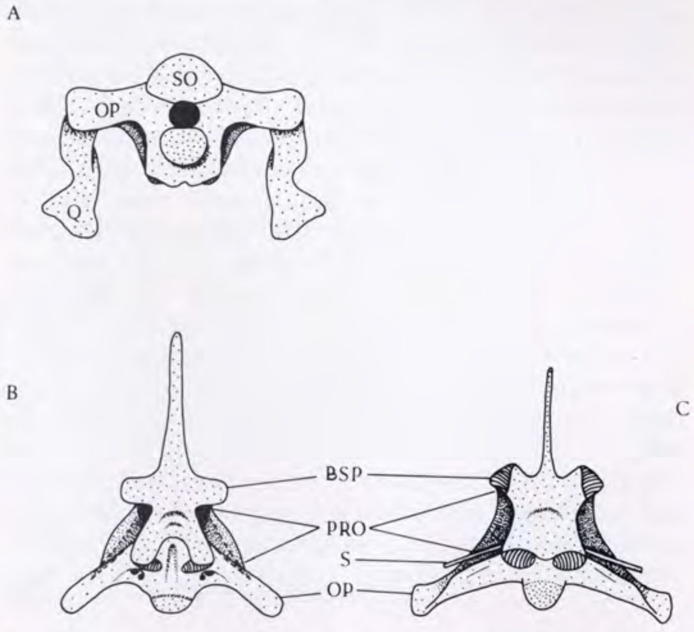


Figure 29. A & B, *Massospondylus*. From photographs of the specimen K1314 in the South African Museum; C, *Dromaeosaurus*. From a photograph in Colbert and Ostrom (1958).

On the thecodont line the picture is somewhat different. The *Youngina* parasphenoid is a rather different shape from that of *Milleropsis*; it too could be derived from that of *Petrolacosaurus*. In both animals there is a pair of parabolic depressions in the ventral surface of the parasphenoid plate, and this pattern tends to persist through the Proterosuchia to some of the dinosaurs, a possible inference being that the parasphenoid as such tends to be retained in these archosaurs. The depressions in the parasphenoids of *Kuehneosaurus* and *Icarosaurus* would tend to reinforce the identity of this element based on the teeth.

Figure 29 shows two dinosaur braincases which look to be extraordinarily primitive in their closeness to the proterosuchian condition. A and B are of *Massospondylus*, an upper Triassic Prosauropod, drawn from photographs of the specimen (S. A. Museum No. K1314). C is of *Dromaeosaurus* (Colbert and Ostrom, 1958), an upper Cretaceous theropod (drawn from published photograph). *Camarasaurus* (Ostrom and McIntosh, 1966), a Jurassic to Cretaceous sauropod, also conforms to this primitive pattern. What is not clear in these seemingly primitive dinosaur braincases

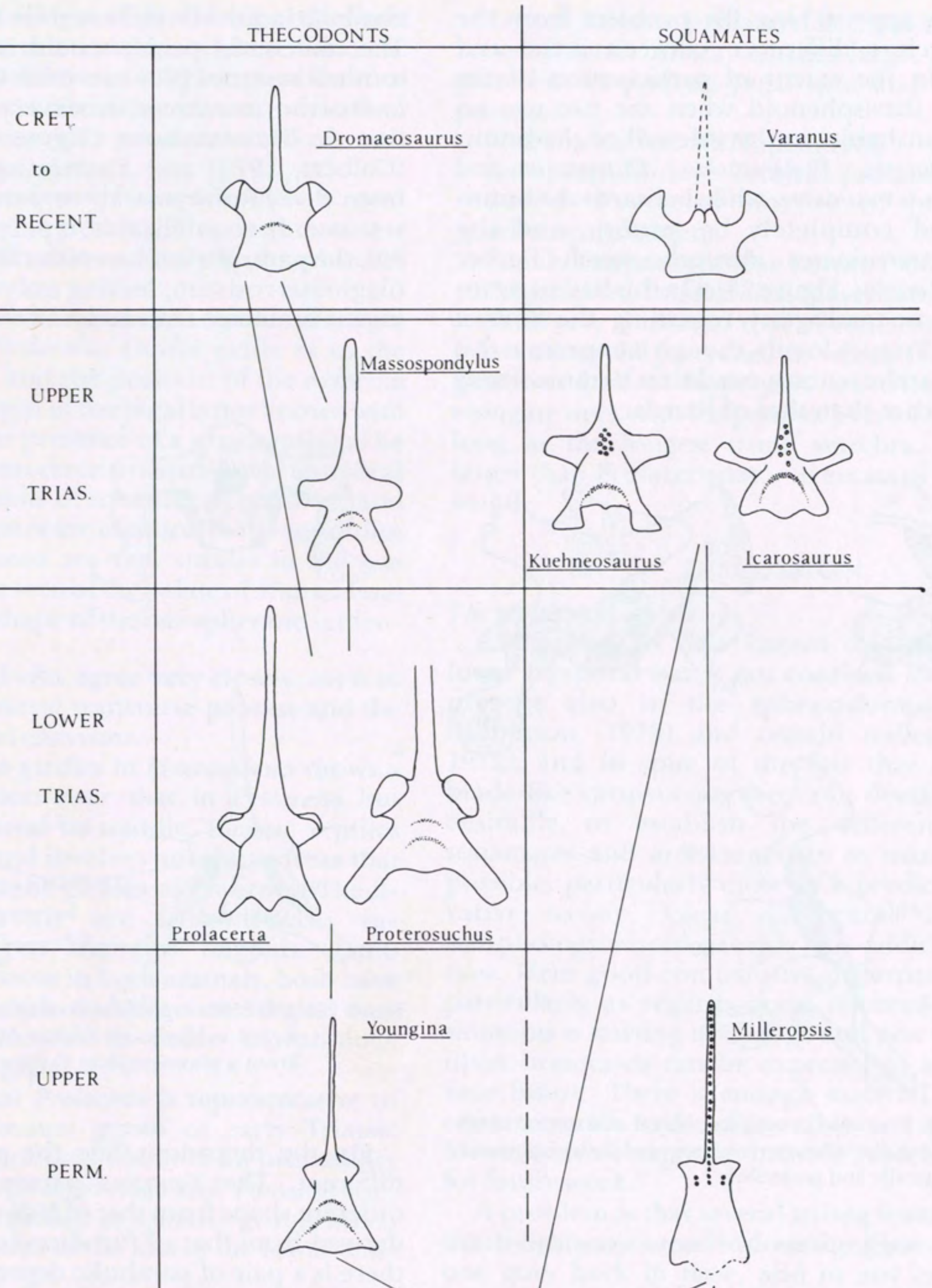


FIG. 30

Figure 30. An attempted separation of thecodonts and squamates through time based solely on ventral views of the para-basisphenoid. The several possible interpretations of the position of *Milleropsis* do not affect the overall picture. *Heleosaurus* is a better archosaur ancestor than *Youngina* but there is no difference in the parasphenoids of the two. The lack of Permo-Triassic lizards is clear.

is the extent of participation of the basisphenoid in the sidewall of the braincase, but with good material in existence this information should soon become available.

In the present context the position of *Euparkeria* is still not clear. Ewer's (1965) drawing of the basisphenoid seems open to question.

Another area where one might expect to be able to make meaningful comparisons is the middle ear region. In *Milleretta* and *Youngina* the region of the fenestra ovale is a large irregular opening bordered by good edges of proötic, opisthotic, basioccipital, para- and basisphenoid. The pattern of exits for cranial nerves IX to XII is primitive; in *Milleretta* IX—XI and jugular vein emerge between exoccipital and opisthotic, XII through the opisthotic (Gow, op. cit.). *Youngina* is similar except that the foramen for XII discharges externally into that which transmits IX to XI and jugular. The stapes of *Milleretta* is peculiar, but that of *Youngina* has the typical rod shape of later sauropsids and runs out under the paroccipital process towards the back of the head of the quadrate.

Typical lizards are characterized by the presence below the foramen ovale of a foramen rotundum, the former bordered anteriorly by proötic, the latter piercing the opisthotic alone. In iguanids these formina are separated by the crista interfenestralis of the opisthotic, in varanids both are anterior to that sheet of bone. The footplate of the stapes is applied against the foramen ovale while a membrane at the foramen rotundum compensates for vibrations of the stapes (Romer, 1956; Robinson, 1973). According to Robinson the required physical effect is attained in *Sphenodon* as follows:

> "an unossified portion of the inner wall of the otic capsule, and the large vagus foramen, serve to allow compensatory movements of the fluids of the inner ear, and probably *Kuehneosaurus* had a condition similar to *Sphenodon* in these respects."

This leads to consideration of the fact that in a typical lizard the otic capsule is encased in bone and this is what makes the foramen rotundum necessary. In *Milleretta, Youngina*, and the early thecodonts listed above the otic capsule is either known, or can safely be inferred, to be open internally.

In crocodiles and birds in which the middle ear is enclosed in bone a foramen pseudorotundum is developed to perform the necessary compensatory movements (Romer, 1956; Baird, 1970; Walker, 1972). In this context the importance of Walker's work on *Sphenosuchus* is that he was able to demonstrate the presence of a foramen pseudorotundum in an upper Triassic pseudosuchian.

Another feature which distinguishes lizards from archosaurs is the extent of the contribution of the parasphenoid/basisphenoid to the sidewall of the braincase. In *Milleretta* the parasphenoid plate is flat, in *Youngina* the lateral edges are slightly upturned. In *Prolacerta* this upturning is pronounced, with a lateral ridge of parasphenoid contacting the proötic, while in *Proterosuchus* contact between parasphenoid and proötic is complete. An extension of this condition can be seen in for example *Stagonolepis* (Walker, 1961) and *Euparkeria* (Cruickshank, 1970). By contrast it appears that in lizards the basisphenoid remains essentially a flooring plate giving no significant contribution to the sidewall of the braincase, which is formed entirely of proötic and opisthotic—this is true of *Varanus* (Bahl, 1937 and personal observation) and *Ctenosaurus* (an Iguanid, Oelrich, 1956). A crista lateroventralis in some lizards gives an impression of lateral depth of basisphenoid, but this is simply a downwardly projecting ridge (Säve Säderbergh, 1947, Figure 9A). The question of changes in the ventral extent of the opisthotic becomes difficult due to fusion of that bone with exoccipital; hence para/basisphenoid morphology is possibly the best indicator of reptilian relationships in the lower Triassic particularly.

The order Thecodontia is considered basal to all later archosaurian radiation. A spate of recent work on the classification of these animals is brought together by Romer (1972c). In Romer's tentative classification we have a suborder Proterosuchia containing four families. Now it is striking that in the Proterosuchidae the archosaurian antorbital fenestra is rather poorly defined (having formed in a thin-boned minimum stress area) and does not yet show the strengthened outlines of more advanced forms. In the light of the above it seems reasonable to assume that the earliest thecodonts lacked the antorbital fenestra and possibly to include a fifth family, the Prolacertidae.

To do this purely on the basis of dermal bones might never prove entirely convincing, but reinforced by what is now known about braincases such an arrangement could make sense. The braincase is well known in *Prolacerta* and *Proterosuchus,* it is reasonably well figured and described in ventral view for *Chanaresuchus* (Romer, 1971) which seems reasonably primitive (further description of this braincase is necessary). Virtually nothing is known of the braincase in Erythrosuchids and Prestosuchids, with genera like *Mandasuchus* being little more than words on paper. The braincase of phytosaurs (Camp, 1930) and aetosaurs (Walker, 1961) is well known; these are fairly advanced in several respects, notably in the presence of a laterosphenoid.

Of Romer's Pseudosuchia the braincase of *Euparkeria* (Cruickshank, 1970) is fairly well known, and considerably more primitive than that of Phytosaurs and Aetosaurs though somewhat advanced over that of the Proterosuchids. Of the Ornithosuchidae the braincase is very inadequately known, though the close proximity of the basal articulations of the pterygoids in *Gracilisuchus* (Romer, 1972a) and *Ornithosuchus* (Walker, 1964) suggest similar specialisations which might be reflected in several other aspects of braincase morphology.

Among Romer's miscellaneous Pseudosuchia is *Lewisuchus*. Romer's (1972b) figure and description of the braincase of this animal seem open to a different interpretation: the possibility exists that there is no laterosphenoid, that the notch for V in the proötic has closed and that Romer's V should be VII.

As far as other later groups of archosaurs are concerned there is a certain amount of information on the braincase in the Crocodilia (fossil and recent) and birds (Walker, 1972), but one wonders whether discussion of this material, *in vacuo* as it were, need be taken too seriously. Little is known about dinosaur origins or of the braincase in the different lines. There is enough to suggest that the Prosauropod braincase was exceedingly primitive (Figure 29A and B), so much so that it is probably derivable only from the Proterosuchian level. The same may be true of theropods based on what little information there is on the braincase in the upper Cretaceous *Dromaeosaurus* (Figure 29C). It seems reasonable to suggest from this that the Saurischia are derivable only from the Proterosuchia. A little more work on existing material will establish this point.

Nothing can be said at this stage about the Ornithischia, though here again good material exists and awaits only description.

The foregoing is a tentative outline of the importance of archosaur braincases in phylogeny and is offered here in the hope of stimulating further work of this nature. These are deep structures well obscured by other bones, but they can be removed successfully and the suggestion is made that where possible braincases be illustrated in lateral, ventral, occipital and saggital and frontal views.

NOTE: I have recently had the opportunity to examine a good braincase of *Euparkeria*. The similarity between the proötics and the foramen for VI in anterior view between *Proterosuchus* and *Euparkeria* is clear from Figure 26 and Figure 37.

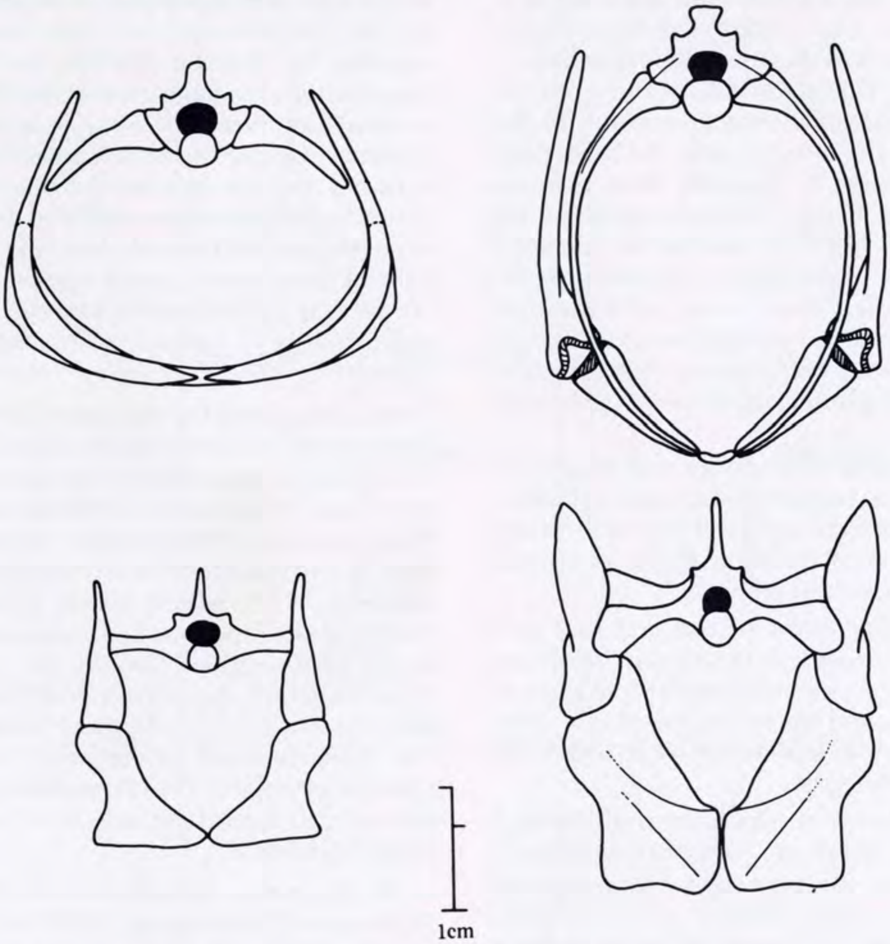


Figure 31 depicts the girdles of *Youngina* (left) and *Prolacerta* (right); all but the pectoral girdle of *Prolacerta* in anterior view, the latter as seen from behind. This gives a clear impression of dorsoventral flattening in *Youngina* and lateral flattening in *Prolacerta*. In order to see how body shape relates to way of life the fossil forms are compared in Table I (page 98) with a selected number of extant forms; when girdle measurements are converted to ratios the animals form an interesting series. This lends itself to misinterpretation as the broad pectoral girdle of crocodiles and *Youngina* is associated with vertical carriage of the humerus and probably does not as such relate to aquatic habits. Bakker's (pers. comm.) thoughts on this aspect are far advanced so it will not be pursued here. Likewise it is misleading to compare the agile *Prolacerta* and slow moving chamaeleon too closely, though the more closely spaced glenoids clearly afford climbers better balance.

## SUMMARY

1. The osteology of *Youngina capensis* is described in detail. There is every indication that this was a terrestrial animal. *Youngopsis* and *Youngoides* are relegated to junior synonyms. No tidy phylogenetic associations are proposed either backwards or forwards in time; there are objections to close association with *Prolacerta*, squamates and archosaurs.
2. The complete osteology of *Prolacerta* is described. A description of the braincase of *Proterosuchus* is included for comparison. It is shown that *Prolacerta* was a swift bipedal animal morphologically very close to the proterosuchian thecodonts, which was probably on a direct line to *Macrocnemus* at least among the lizard-like forms of the European middle Triassic. *Pricea* is relegated to a synonym of *Prolacerta*.
3. Discussion of sauropsid braincases suggest fundamental differences exist between those of lizards and thecodonts—a situation which helps to dispel the concept of *Prolacerta* as an ancestral squamate.

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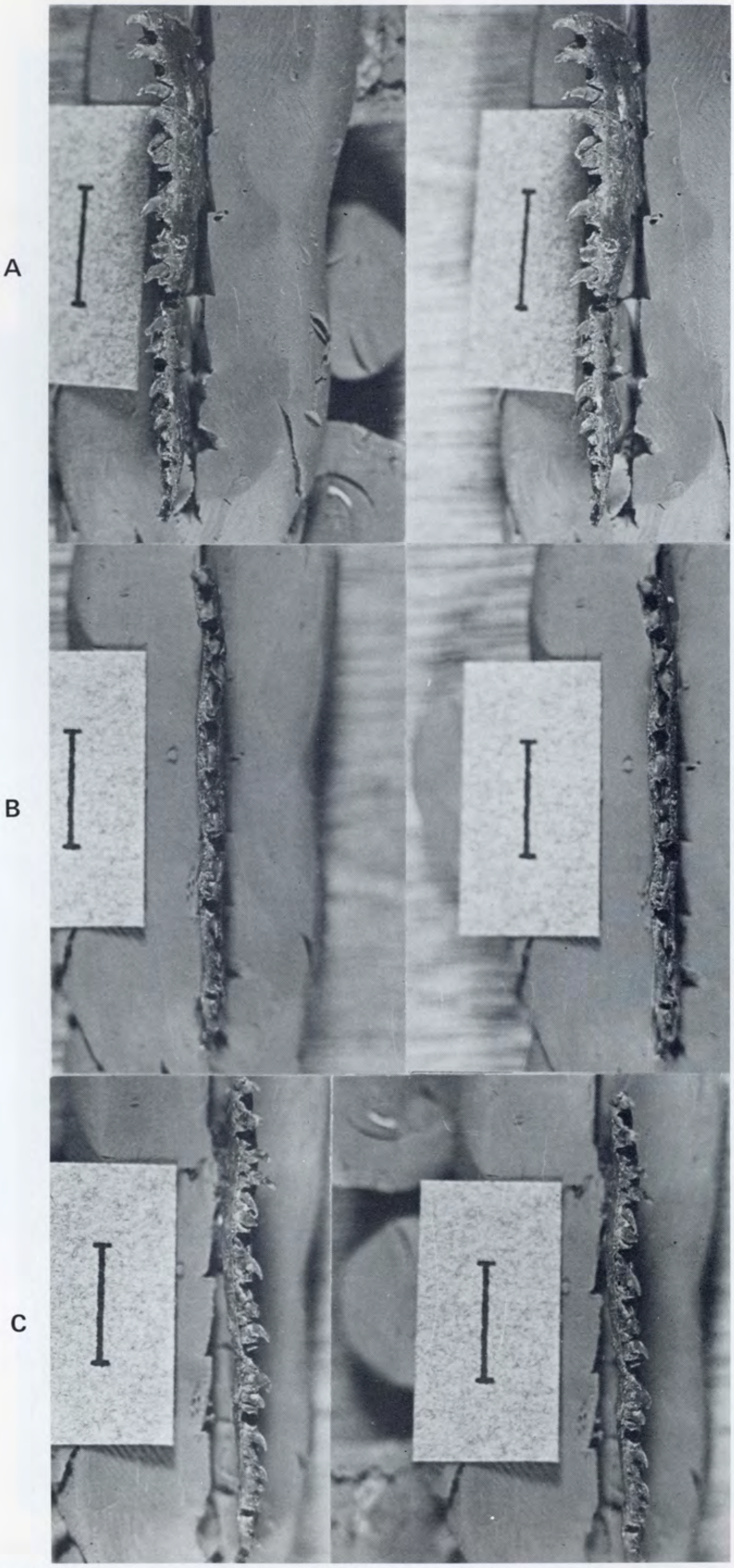

Figure 32. Stereo-photographs of left maxilla of *Prolacerta broom* B.P.I. 2675. A, Labial oblique; B, Straight occlusal; C, Lingual oblique. Scale is 1 cm long.

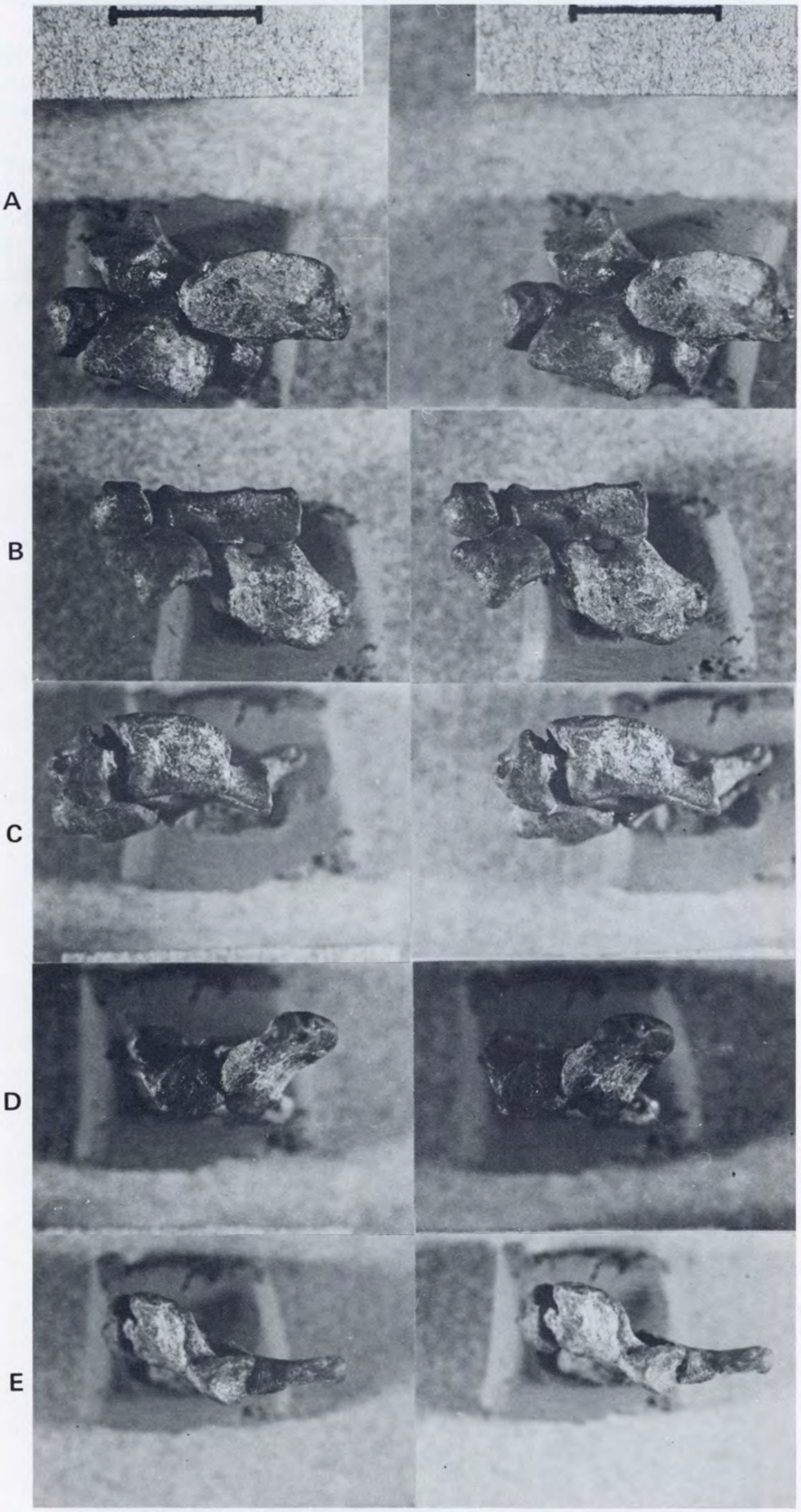

Figure 33. Stereo-photographs of ankle of *Prolacerta broomi* B.P.I. 2675. A, Ventral; B, Dorsal; C, Normal to tibial facet; D, Normal to fibial facet on astragulus; E, Both facets oblique. Scale is 1 cm long.

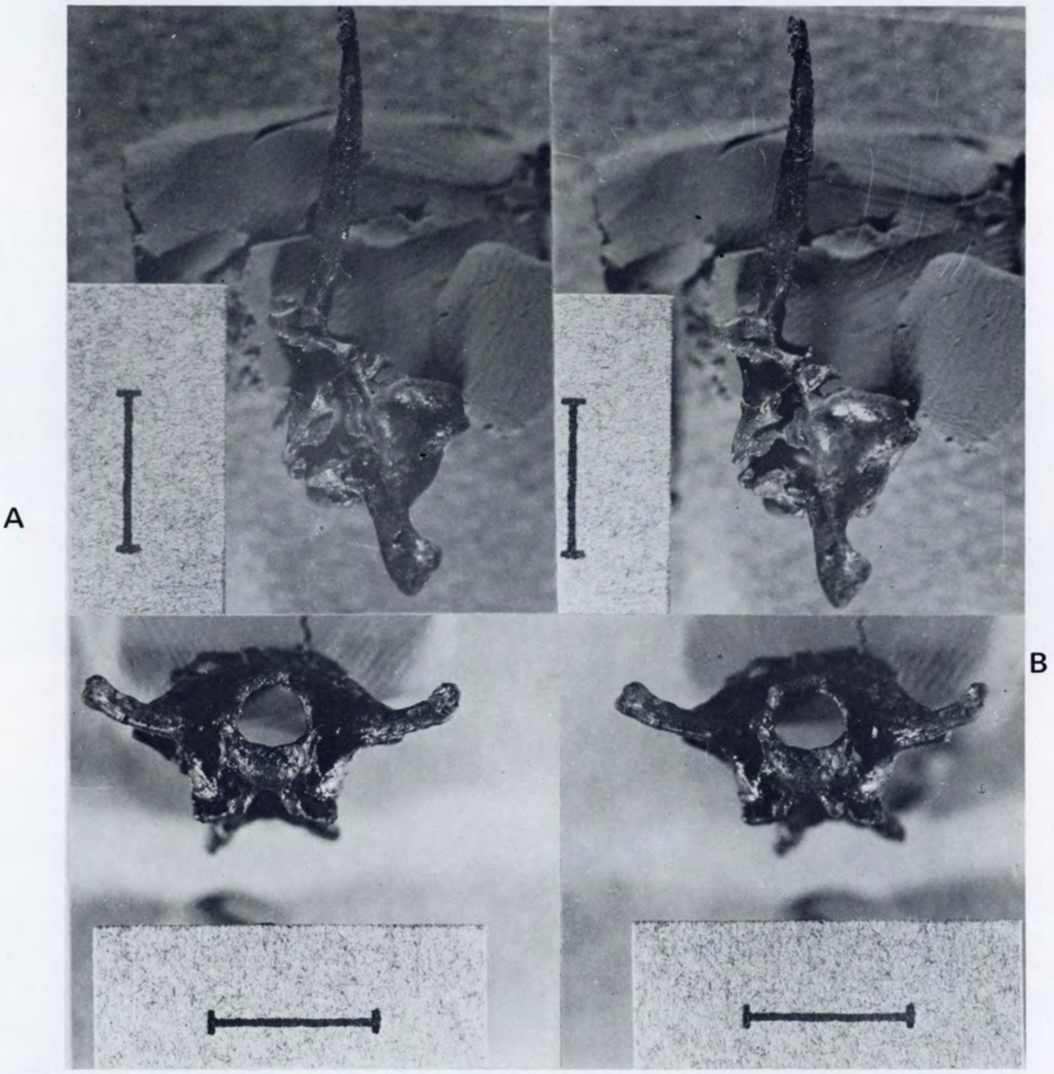

Figure 34. Stereo-photographs of braincase of *Prolacerta broomi* B.P.I. 2675. A, Left lateral view; B, Posterior view. Scale is 1 cm long.

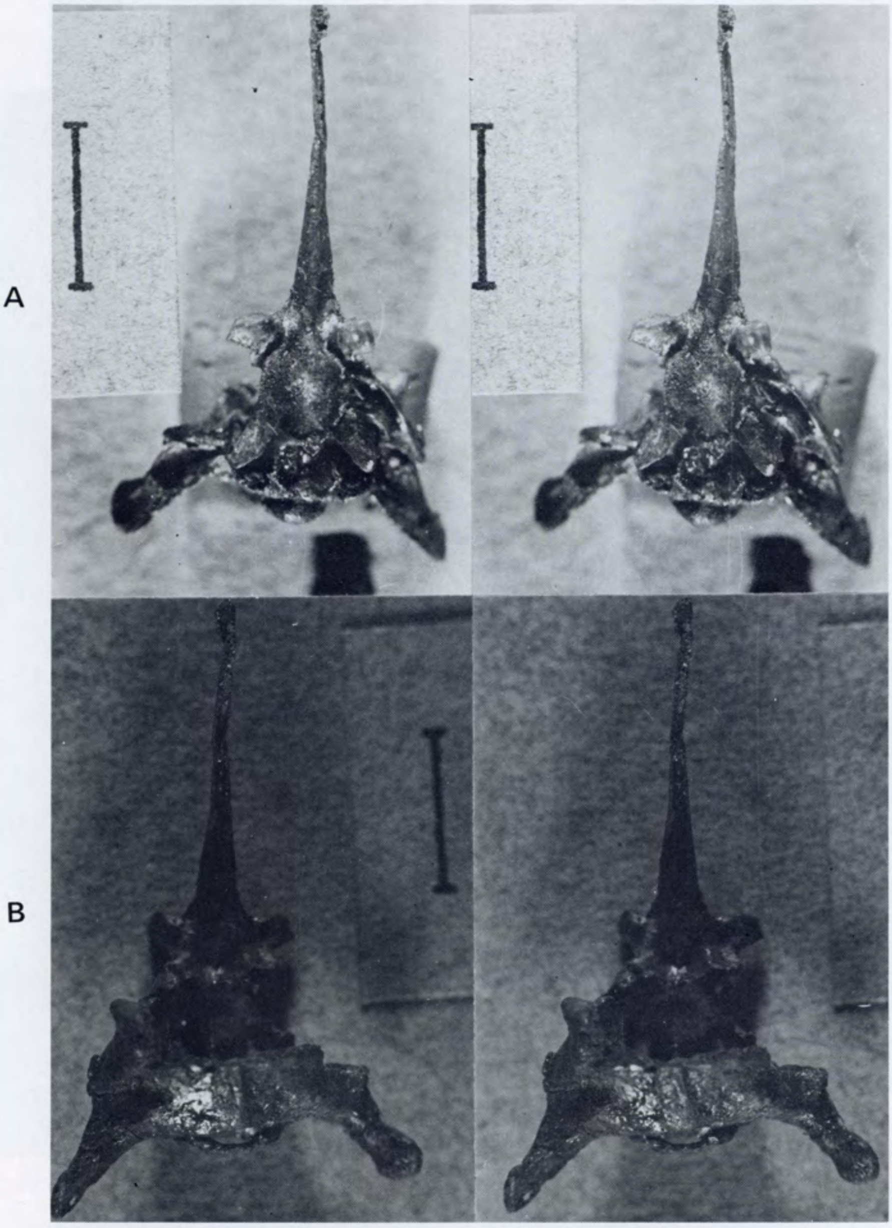

Figure 35. Stereo-photographs of braincase of *Prolacerta broomi* B.P.I. 2675. A, Ventral view; B, Dorsal view. Scale is 1 cm long.

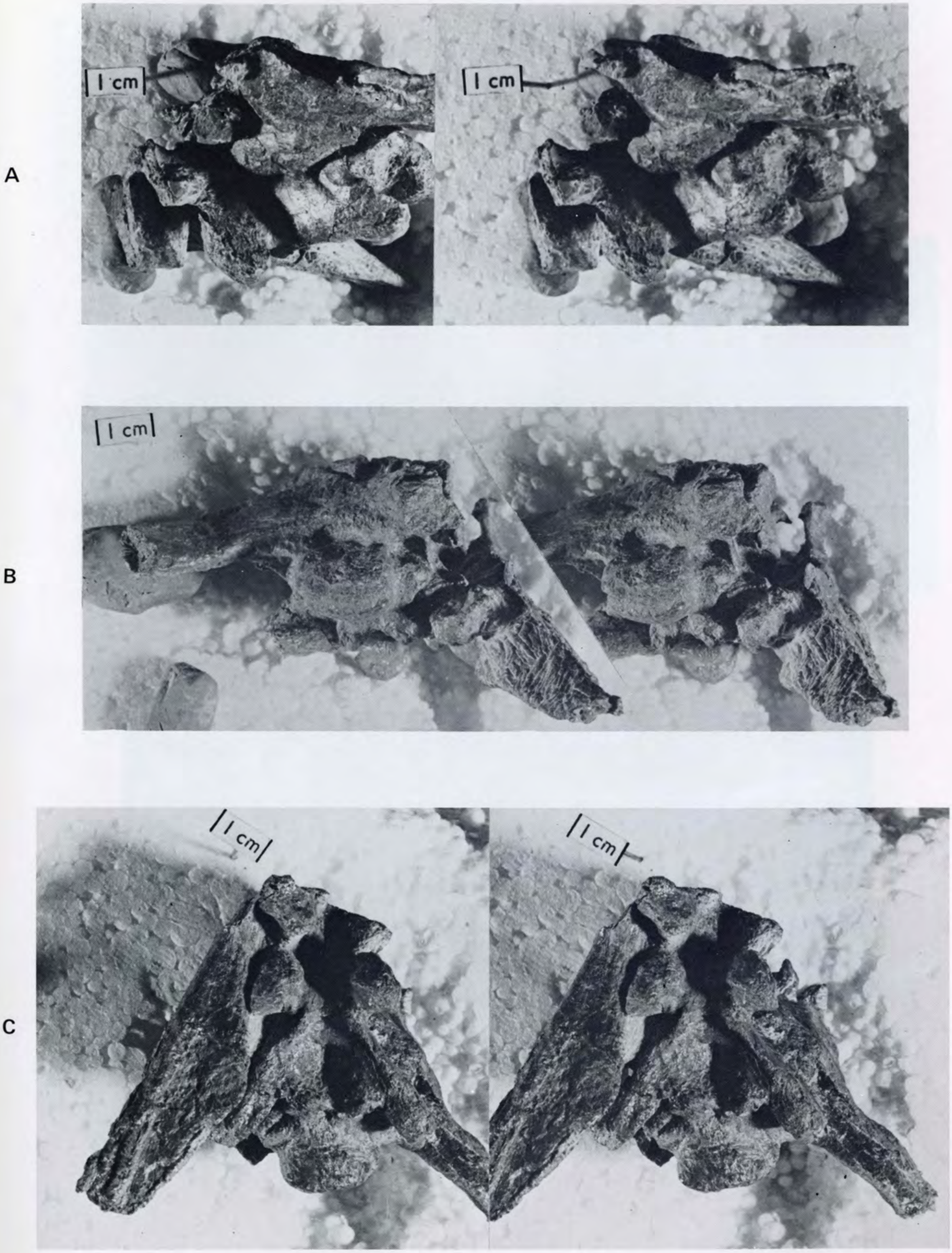

Figure 36. Stereo photographs of braincase of *Proterosuchus fergusi* B.P.I. 3993. A, Left lateral; B, Posterior; C, Ventral. Scale is 1 cm long.

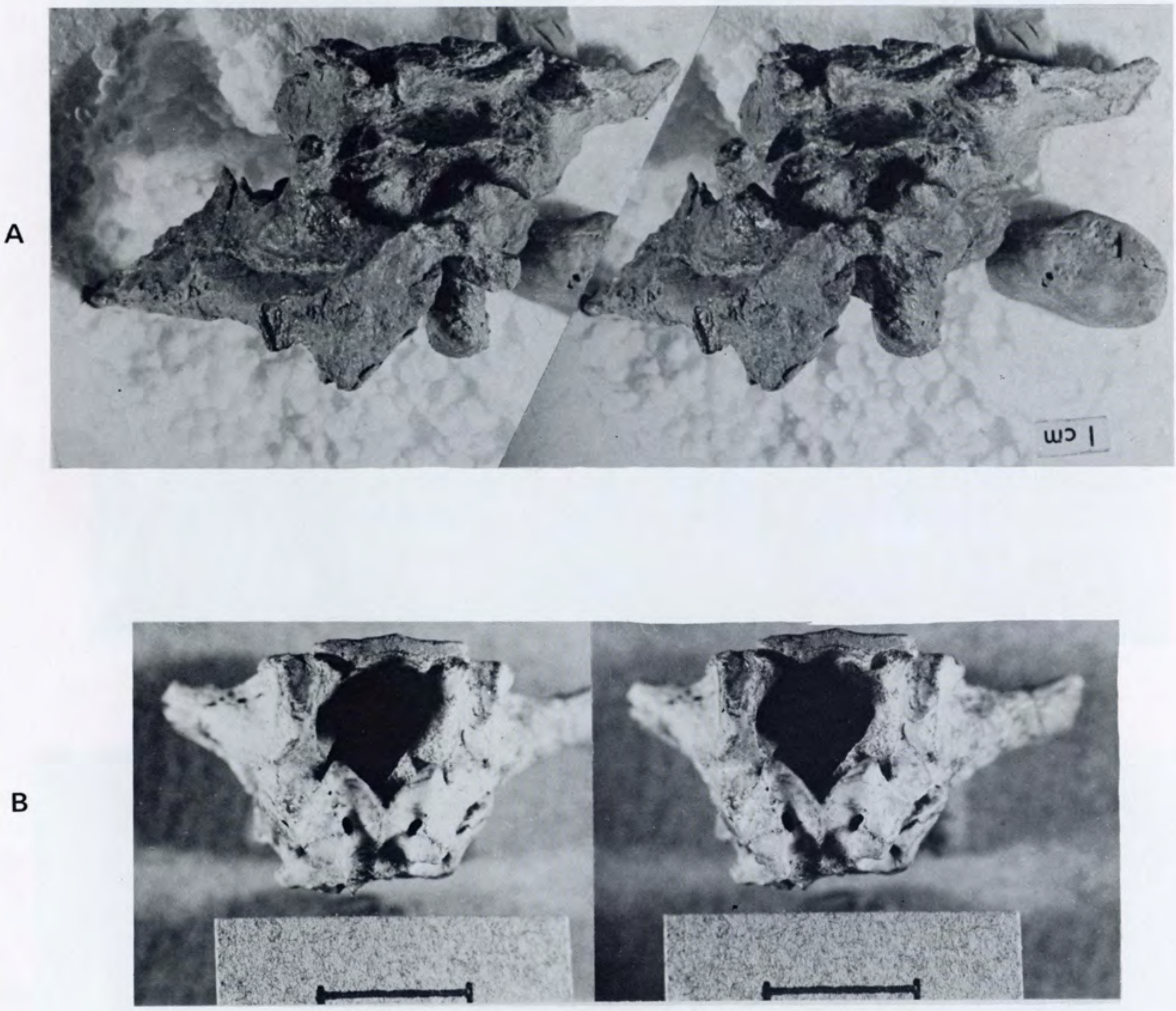

Figure 37. Stereo-photographs of: A, Braincase of *Proterosuchus fergusi* B.P.I. 3993, anterior view; B, Braincase of *Euparkeria capensis* S.A.M. 7696, anterior view. Scale is 1 cm long.

# ABBREVIATIONS

A. —angular
al.pr.bsp. —alar process of basisphenoid
al.pr.pro. —alar process of proötic
ART. —articular
BO. —basioccipital
BSP. —basisphenoid
bpt.pr. —basipterygoid process
b.t. —basal tubera
cpr. —crista proötica
ds. —dorsum sella
EO. —exoccipital
EPT. —epipterygoid
F. —frontal
f.o. —foramen ovale
f.m. —foramen magnum
J. —jugal
j.f. —jugular foramen
L. —lacrimal
MX. —maxilla
N. —nasal
OP. —opisthotic
P. —parietal
PAL. —palatine
PMX. —premaxilla
PO. —postorbital
POF. —postfrontal
PP. —postparietal
PRF. —prefrontal
PRO. —proötic
PR.ART. —prearticular
PSP. —parasphenoid
PTDG. —pterygoid
P. —parietal facet
p.a. —pila antotica
par.proc. —paroccipital process
p.pr.pro. —posterior process of proötic
Q. —quadrate
QJ. —quadratojugal
q.ra.pt. —quadrate ramus of pterygoid
ro.psp. —parasphenoid rostrum
S. —stapes
SA —surangular
SO. —supraoccipital
SPL —splenial
SQ. —squamosal
ST. —supratemporal
T. —tabular
V. —vomer
v.c. —vidian canal