

A NEW PROTOSUCHIAN CROCODILE FROM THE UPPER TRIASSIC ELLIOT FORMATION OF SOUTH AFRICA

by

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ABSTRACT

A new protosuchian crocodilian, *Baroqueosuchus haughtoni* from the Upper Triassic or Lower Jurassic Elliot Formation of the Orange Free State is the most primitive protosuchian crocodilian known. There are no contacts between the quadrate and opisthotic or below the cranio-quadrate canal, the internal carotid arteries were not enclosed in separate foramina and the basicranium was flat, with the basisphenoid being broadly exposed on the base of the skull. The basic diagnosis of the Order Crocrodilia is discussed and a new diagnosis is offered based upon cranial anatomy.

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INTRODUCTION

The predominantly Triassic (see below) Elliot Formation of South Africa has produced several genera of protosuchian crocodilians and possibly related thecodonts including a new and primitive protosuchian crocodilian. The most complete and best known protosuchian is *Orthosuchus stormbergi* (Nash 1968, 1975), while *Notochampsa istedana* (Broom 1904, Haughton 1924), *Pedetecosaurus levisi* (van Hoepen 1915, Bonaparte 1972) and *Erythrochampsa (Notochampsa) longipes* (Broom 1904, Haughton 1924) are poorly preserved or poorly prepared. *Sphenosuchus acutus* (Haughton 1924, Walker 1972) has a number of synapomorphies with some thecodonts (*Hesperosuchus* and *Pseudhesperosuchus*, Bonaparte 1971) and may have some crocodilian synapomorphies (see below) though its affinities with the crocodilia not yet clear; this problem is beyond the scope of this paper and will be treated in a paper on protosuchian systematics and anatomy (Busbey in prep).

The new protosuchian described herein reveals details of the otic region and suspensorium that were previously unknown (and to some extent unrecognised) and permits an evaluation, based upon cranial characters, of some of the controversy surrounding protosuchian systematics.

The Elliot Formation (formerly the Red Beds of the Stormberg Series) has classically been thought of as being entirely Triassic. Recently Olsen et al (1982), as part of a paper correlating the Newark Supergroup of the Newark Basin, suggested that the entire upper Elliot Formation and the Clarens Formation (formerly the Cave Sandstone) are entirely Jurassic in age. (See also Olsen and Galton, this volume). The correlation is based on radiometric dates of the Drakensberg volcanics, that overlie the Clarens Formation in the east but interfinger with the Clarens Formation in the West, and on reptile skeletal and footprint assemblages. A paper referenced in support of this reassignment is Clemens et al. (1979), in which neither reptile skeletal or footprint assemblages are discussed. In

fact, the work of Olsen and Galton (1977) is referred to in Clemens et al. (1979), only to the extent of acknowledging the possibility that the upper Elliot and Clarens Formations might be lower Jurassic. In their paper they provide no evidence to support Olsen and Galton (1977) or Olsen et al. (1982).

Olsen and Galton (1977) note that radiometric age dates of the Drakensberg volcanics from Fitch and Miller (1971) are said to be 181 and 165 My BP. However, Fitch and Miller (1971) actually report a date of 187 ± 7 My. This provides a minimum estimate of the initiation of Drakensberg vulcanism for more southern localities where the samples were collected. Based on their reconstructed rates of deposition they suggest that the Elliot Formation is $187-193 \pm 7$ My. old. The disparity between the ages reported in the actual article and those mentioned in Olsen and Galton (1977) are difficult to understand; it is sufficient to note that the estimated dates for the deposition of Elliot sediments are much earlier based on the original data in Fitch and Miller (1971) than from the re-estimates by Olsen and Galton (1977). Evidence that Olsen and Galton (1977) considered to be decisive for an early Jurassic date of the upper Stormberg is the presence of the prosauropod *Anchisaurus* from Olsen's Zone 3 of the Newark Basin and from the Clarens Formation of South Africa. *Anchisaurus* is not found in the Elliot Formation, and thus has no bearing on the age of the deposits from which most of the protosuchians are known. Other problems in correlation between the Newark Basin and South Africa are a lack of latest Triassic semionotid fish and footprint assemblages for comparison. We are merely told in Olsen and Galton (1977) that the fish and footprint assemblages compare favourably with earliest Jurassic assemblages. Until a stronger case is made we acknowledge the possibility of an earliest Jurassic date of the upper Elliot Formation, but will continue to consider it as latest Triassic.

The new protosuchian is known from two partial braincases. BP-1-4746 was found by Dr. J.W. Kitching in 1978, while conducting preliminary field collections from the Clarens and Elliot formations on the farm Sunnyside (1178) near Clarens in the Orange Free State, along the northern border of Lesotho. BP-1-4746 is represented by the posterior half of a skull missing the distal ends of the quadrates, the 'cheek' bones, the lateral edges (to varying degrees) of the squamosals, and the left postorbital. It was heavily encrusted in a haematite-cemented sandstone that was mechanically removed. The second specimen, BP-1-4946, was found in 1980 by C.E. Gow on the farm Damplaats (55), in the Orange Free State, in the Upper Elliot Formation. It was found with a collection of rolled postcranial bones mixed with a fabrosaurid skeleton. This same locality also yielded the advanced cynodont *Tritylodon* and the ubiquitous prosauropod *Massospondylus*. BP-1-4946 constitutes the posterior half of the skull with quadrates in position. It was encased in soft calcareous red mud-

stone with very little haematite adhering to the bone. The nearly complete left and partial right squamosals were heavily encrusted with haematite and had become dissociated prior to burial and fossilized separately. Distortion has pushed the left side of the braincase inwards; concomitant plastic deformation has particularly affected quadrate morphology. Mechanical preparation of the braincase was taken as far as possible. The right quadrate was removed and completely cleaned with N/10 formic acid. The squamosals were partially cleaned of haematite through prolonged treatment with thioglycolic acid (Rixon 1976). Detailed preparation of the braincase was achieved through the careful use of N/10 formic acid dropped onto small areas at a time. Spent acid was withdrawn using tissue paper and replaced with fresh acid until the desired degree of penetration was obtained.

Institutional abbreviations used are:-

- BP Bernard Price Institute for Palaeontological Research, University of the Witwatersrand.
MCZ Museum of Comparative Zoology, Harvard University.

SYSTEMATICS

The Order Crocodylia

Unfortunately there is no clear consensus about what constitutes a crocodylian. We thus offer a discussion of some current problems and a new diagnosis of the crocodylia based on cranial characters primitive for the group.

There is some confusion as to the cranial characters that are unique to the crocodylia (Walker 1970, 1972, 1974, Whetstone and Martin 1979, Tarsitano and Hecht 1980, Crompton and Smith 1980). The problem is also embroiled in debate about the phylogeny of birds and the phylogenetic relationships of primitive archosaurs. In so far as the protosuchians are concerned the confusion is due in part to:

1. Lack of data about definitive cranial characters of protosuchian crocodylians.
2. Misinterpretation of the morphology of protosuchian crania.
3. The tacit use of modern eusuchian character states as being typical of all fossil crocodylians.
4. A lack of outgroup comparisons with non-crocodylian archosaurs.

Langston (1973) presented an extensive summary list of characters that are presumably primitive for crocodylians. Because of the incomplete nature of most protosuchian material it is not possible to use all of the characters on any one genus. The cranial characters that he listed that have the potential to be seen in most protosuchians are:

1. The flat ornamented skull deck.
2. Strongly inclined quadrates, bordered anteriorly by a long, slender quadratojugal.
3. Akinetic palate (i.e., basipterygoid articulation closed) pterygoids with wide and deep wings (transverse processes).
4. Many cranial bones, including articular, more or less pneumatic.
5. Eustachian passages more or less enclosed in bone.
6. Posttemporal fenestra reduced.
7. Squamosal, quadrate, and paraoccipital process combine to form an otic meatus.

Characters 1,3,4, and 5 are taxonomically significant but require further clarification, characters 2 and 7 do not appear in early protosuchians, and character 6 is widely distributed amongst various archosaur taxa and may be of little utility.

Walker (1970, 1972, 1974) has published classifications and lists of characters (with subsequent modifications) that we feel significantly broaden and at the same time distort the concept of the crocodilia as a natural group; this was done to include *Sphenosuchus acutus* within the crocodilia. Walker's classification thus contains a confusing mixture of characters, some of which are primitive for archosaurs, some which seem to be autapomorphic for non-crocodilian lineages, some which may be based on faulty interpretation of the morphology of *Sphenosuchus acutus* (see discussion below), and some which may indeed be synapomorphic for protosuchians and sphenosuchids. His taxonomic categories are based upon very poorly known protosuchian genera (*Stegomosuchus*, *Pedeticozaurus*, *Hallopus*) and include diagnoses that contain characters not known for these genera. The holotype of *Stegomosuchus*, from the Connecticut Valley, is only minimally prepared (see Lull 1953 and sketch in Olsen 1980) and demonstrates few diagnostic cranial characters. *Pedeticozaurus* is known only from the holotype, which is an impression in fine sandstone, with a partial steinkern of the right otic meatus, and has only two characters that may suggest it is a crocodilian (shape of the otic region as revealed by the steinkern — Bonaparte 1972; and possibly elongated carpals, but see Nash 1975). *Hallopus* seems to have elongated carpals, but there is insufficient diagnostic material for specific assignment and no cranial material and for the time being the name should apply only to the type. Walker's broader category, the order Crocodylomorpha, includes forms that do not possess diagnostic crocodilian features. We shall discuss some of these characters below.

Recently Tarsitano and Hecht (1980) have reviewed the relationships of *Archaeopteryx*, and are highly critical of the recent studies of Walker (1970, 1972, 1974) and of Ostrom (1976). They also address the problem of crocodilian relationships and are highly critical of most of the characters listed by Walker. They dismiss most of the characters Walker used. Though we agree in prin-

ciple and to some degree in part with their analysis in regard to the relationships of crocodilians (that *Archaeopteryx* is not closely related to crocodilians and that the affinities of *Sphenosuchus* are not clear), many of the criticisms are made as unsubstantiated or incorrect assertions. We shall only address some of those points concerning protosuchian cranial characters in this paper.

Tarsitano and Hecht (1980) maintain that the following characters, listed by Walker, are actually primitive for archosaurs;

1. Possession of laterosphenoids.
2. An external mandibular fenestra.
3. Antorbital fenestrae.
4. Crescentic occipital surface.
5. Short paroccipital process projecting behind the quadrate forming the posterior wall of the tympanic cavity.
6. Carotid circulation based upon paired grooves and pneumatic basisphenoid.
7. Elongate cochlear duct.

We shall discuss characters 6 and 7 below. Laterosphenoids are clearly not primitive for thecodonts. *Chasmatosaurus* and *Euparkeria* do not possess laterosphenoids (Cruickshank 1970) and their braincases are not derived over those of more primitive non-theodont diapsids. Characters 2 and 3 appear to be primitive for archosaurs, as stated, but character 4 is sufficiently vague to be of little use, since it is the composition of the occipital crescent and not the overall shape that is important. Character 5 may be primitive for diapsids and requires both further elaboration and study.

Tarsitano and Hecht (1980) provide their own list of primitive cranial characters for the Crocodilia and evaluate the characters deemed important by Walker:

1. crocodilian eustachian (pharyngotympanic) tubes;
2. forward sloping quadrate;
3. crocodilian otic notch;
4. sculptured dermal bones;

They do not provide more detailed definitions of these four character states. For example, the reference on the crocodilian pharyngotympanic system (Colbert 1946) is merely a description of the morphology in a few modern crocodilians. They have made no attempt to extract useful characters from their source. The 'forward sloping quadrate' is of little use, since the quadrate slopes forward in many thecodonts (for example, see *Proterosuchus* (*Chasmatosaurus*), original photographs or sketches, not the reconstruction of Cruickshank 1972, and *Proterochampsia*, Sill 1967), and in primitive protosuchians it is actually fairly vertical (see *Hemiprotosuchus*, Bonaparte 1971, and the new genus below). No explicit definition is given of the characters involved in the 'crocodilian otic notch' (based on comments later in their paper they implicitly

mean modern morphology and thus concur with the character state as given by Langston); yet the protosuchian otic notch lacks many of the specializations of more derived crocodilians (Busbey, in prep). In short, without further elaboration this list of undefined characters has little utility.

Tarsitano and Hecht (1980) state that the quadrate of any true crocodilian must possess all of the contacts of the quadrate of a modern crocodilian; this includes opisthotic contacts above and below the cranioquadrate canal. No currently accepted protosuchian genus possesses all of the contacts present in 'modern' crocodilians and even metriorhynchid and teleosaurid 'mesosuchian' crocodilians do not possess a contact between quadrate, squamosal, and opisthotic behind the tympanum (Eudes-Deslongchamps 1863, Antunes 1967, de Gasparini and Dellape 1976, Wenz 1968, Nash 1975). And furthermore, the quadrate and body of the opisthotic fail to meet below the cranioquadrate canal in several primitive protosuchian genera (see below). Thus, Walker (1972) was correct for primitive protosuchians (and apparently spheenosuchid thecodonts) — the quadrate did not contact the body of the opisthotic or the paroccipital process behind the tympanum; its contacts were exclusively with the squamosal and side of the braincase.

As Tarsitano and Hecht (1980) point out, the supposedly kinetic skull and possible possession of salt glands in *Sphenosuchus* are based on Walker's interpretations and are hypothetical even for *Sphenosuchus*. Thus these 'characters' cannot be used with any reliability in crocodilian systematics.

Tarsitano and Hecht (1980) note that the path of the internal carotid is also hypothetical in *Sphenosuchus* and therefore has little systematic value (which is true), but in making this assertion they make a sweeping statement about the 'similarity' of the carotid circulation in dinosaurs, thecodonts, and other amniotes without describing the nature of the similarity. They are possibly correct about the pneumatic basisphenoid. This is seen in various carnosaurs (Osborn 1912, Russell 1970), coelurosaurs (Osmolska 1976, Osmolska et al. 1972, Colbert and Russell 1969, Greg Paul, pers comm), and possibly other archosaurs. It does not, however, seem to be a primitive feature (the basisphenoid of primitive thecodonts such as *Proterosuchus* and *Euparkeria* is still primitively shallow and is not pneumatized— and may possibly be related to the depth of the basicranium).

Tarsitano & Hecht (1980) are correct in noting that many archosaurs (we include birds) have an elongated cochlear recess (see also Langston 1960), Whetstone and Martin 1979, Hopson 1979) and that it might not necessarily indicate a close relationship between birds and crocodilians. However, the distribution of this character within the Archosauria is currently poorly known. They further maintain that an enlarged cochlear recess occurs in many groups (see below) and is therefore plesiomorphic for amniotes. The presence of an 'elongated' cochlea in sea turtles and primitive mammals

does not invalidate its use for comparisons within archosaur taxa; there is simply no evidence (see the survey by Hopson 1979) that primitive synapsids (theropsids) or early sauropsids shared an elongate cochlear recess and that this represents an amniote synapomorphy. In many primitive reptiles the floor of the inner ear is unossified and in taxa where it is ossified, for example, in primitive therapsids (Hopson, pers comm.) or *Captorhinus* (Heaton 1979), the cochlear recess is short. In any case, their reference for cochlear size in the sea turtles (based only on *Chelonia midas*) is Wever (1979), who provides data on the length and width of the basilar membrane, auditory papilla, and Organ of Corti, not on the size of cochlear recess itself. While other turtles have basilar membrane lengths of 500 to 1100 microns, *Chelonia midas* has a basilar membrane length of about 1700 microns. This does not compare with a basilar membrane length of over 3700 microns in *Caiman crocodilus* and 4900 microns for *Alligator* and *Crocodylus* which, based on the size of the cochlear recess, may be shorter than that in more derived archosaurs. In fact, in their own paper they are not clear in regard to the significance of the size of the cochlear recess; on page 173, paragraph 4, they state: 'It should be noted that an elongate cochlea is also present in the Prototheria . . . dinosaurs, and sea turtles . . . and is therefore a plesiomorphy', yet on the same page in paragraph 9: 'The distribution of this character state (the elongate cochlea) among outgroup taxa (see above) indicates that it cannot be used as a synapomorphy showing the common ancestry of birds and crocodiles, but rather that it represents an advanced amniote or primitive archosaurian condition'. Is it an archosaurian apomorphy, a mammalian apomorphy, or an advanced amniote apomorphy (whatever is meant by 'advanced amniote')? The occurrence of an enlarged cochlear recess in derived members of several lineages probably represents parallel development of these structures.

Tarsitano and Hecht (1980) also question the significance of the subcapsular process in demonstrating a close relationship between crocodilians and birds. This process extends anteroventrally from the opisthotic, subdividing the primitive metotic fissure into an anterior recessus scala tympani (containing a lateral projection of the perilymphatic duct) and posterior metotic fissure in crocodilians and birds. An analogous structure in therian mammals, the processus recessus, also subdivides the primitive metotic fissure. Again, they state that the distribution of this character is unknown within the Archosauria and that in any case it is plesiomorphic for mammals, reptiles and birds. In so far as the subcapsular process can be recognised, Whetstone and Martin (1979) are partially correct — it can only be identified easily in crocodilians and birds. But the problem is not as circumscribed as this; the basic question is did other archosaurs have a medial projection of the perilymphatic duct that was separated in some way from the primitive metotic fissure? Cruickshank (1970) notes a possible

separate lateral opening for the perilymphatic system (fenestra pseudorotunda?) in the braincase of *Euparkeria* implying the presence of a subcapsular process, but this requires further inspection of the specimen to verify its presence. A fenestra pseudorotunda has been identified in the coelurosaurs *Galimimus bullatus* (Osmolska et al. 1972), and *Dromaeosaurus albertensis* (Colbert and Russell 1969) which makes the projection of the opisthotic dorsal to the opening, a subcapsular process by default. For the present, after an admittedly limited initial literature survey of the inner ears in primitive thecodonts and other dinosaurs, we must partially agree with Tarsitano and Hecht (1980); with the current state of preparation and with the available material, it is difficult to approach this question since this region is poorly ossified or highly modified in the taxa we have seen (various phytosaurs, omithischians, and saurischians). It is significant, though, that a fenestra pseudorotunda has been identified in two coelurosaurs. It would appear from Walker's sketches (he has not published photographs) that *Sphenosuchus* does indeed have a subcapsular process similar in morphology to that of crocodilians and different from that of birds; but there is insufficient published information to allow an evaluation of the ear in related thecodonts (such as *Hesperosuchus* and *Pseudhesperosuchus*) or coelurosaurs.

We take issue with Tarsitano and Hecht's (1980) remarks about the importance of similar embryonic origin of the subcapsular process of processus in mammals, birds, and crocodiles. They maintain that since this process is formed from the basal plate in these groups it represents a plesiomorphy and is therefore primitive for all the groups. The embryonic origin of this process in these groups is of little importance here; it is equivalent to saying that any structure derived from the neural crest is homologous and therefore plesiomorphic for all the groups in which it appears and that it is therefore not useful as a character for phylogenetic analysis. In this instance it is the ultimate expression of the morphogenetic process that is important not the embryonic origin of the tissue. Their point also sidesteps fossil evidence that indicates that such a process was not possessed by therapsids, or even by early mammals (Kermack et al. 1981). They cite the study by Kuhn (1971) on the pouch young of the echidna, noting that a transient structure appears on the anterior face of the metotic fissure separating the metotic fissure and foramen rotundum. They then state that this process is homologous to the processus recessus of therian mammals and represents a synapomorphy for all mammals; it was supposedly lost in the adults of modern monotremes because of aquatic adaptations. Kuhn (1971) is less sure of the homology of this process than are Tarsitano and Hecht (1980); he carefully points out that this transient structure may not be homologous to the processus recessus of therian mammals and in the text and figures denotes this by enclosing processus recessus within quo-

tes.

The most detailed and explicit character list for Crocodilia is that of Crompton and Smith (1980), which is partially compiled from previous sources. We will paraphrase their criteria for the skull:

1. Displacement of the anterior margin of the primary head of the quadrate from its contact with the opisthotic (paraoccipital process) and squamosal onto the prootic and laterosphenoid.
2. Development of extensive secondary contacts between the quadrate and the squamosal behind the tympanic membrane and with the opisthotic below the hyomandibular ramus of the facial nerve.
3. Development of an enlarged eustachian system which penetrates basioccipital and basisphenoid and expands into an extensive system of pneumatic spaces in the basioccipital, basisphenoid, opisthotic, prootic, quadrate, and pterygoid bones.
4. Fusion of the basipterygoid joint with surrounding structures so that the basisphenoid, pterygoid, and quadrate are joined as a solid structure.
5. The suturing of the bones forming the occipital region with the quadrate, squamosal, and parietal into a solid plate. The fused exoccipital and basioccipital expand to close the posterior temporal openings and also expand downwards to establish a secondary connection with the basisphenoid. This latter expansion traps the internal carotid and IX and X nerves in secondary foramina.
6. Change in the primitive position of the external opening of the perilymphatic cistern from the fissura metotica to a new opening, the fenestra pseudorotunda, separated by a broad bony septum from the fissura metotica.

Character 1 is significant, but requires further elaboration and clarification (see new diagnosis below).

Character 2 does not draw an important distinction between two separate regions of contact of the quadrate with surrounding bones. A contact between the body of the opisthotic and quadrate is developed only in some advanced protosuchians and contacts between the quadrate and paroccipital process are not even developed in some longirostrine 'mesosuchians'. (The term mesosuchia is used here in an informal sense, since it refers to a paraphyletic grade of crocodilians). Thus, these are advanced features for crocodilians and do not constitute primitive features for the group (Busbey, in prep).

Character 3 recognises the importance of cranial pneumaticity but it is more specific than this character as listed in Langston (1973). Unfortunately many of the bones mentioned are also pneumatic in birds, coelurosaurs, and carnosaurs (see abo-

ve). Based upon the new protosuchian specimen and study of previously published work, the only unique pneumatic cranial elements of crocodilians are the supraoccipital and parietal. With the addition of these bones to the list in Crompton and Smith (1980), the degree of pneumaticity in crocodilians can be seen to surpass that of birds and saurischian dinosaurs.

Character 4 is also significant, because it recognises the closure of the basiptyergoid articulation and involvement of the quadrates, which does seem to be unique for crocodilians.

Character 5 is partially contingent upon character 2 and is incorrect in its description of how the occiput formed. Since the quadrate and squamosal do not meet behind the tympanum, and in primitive forms (see below) the quadrate and body of the opisthotic are not in contact, the condition they list here is actually derived beyond protosuchians, teleosaurs, and metriorhynchids. The closure of the posttemporal fenestra was brought about by the posterior extension of the squamosals and their contact along the entire length of the paroccipital processes. It would also appear (Busbey, in prep) that it was the rotation of the quadrate and flexure of the basicranium that closed up the space between the quadrate and opisthotic, not a downward expansion of the exoccipital and basioccipital. In the most primitive protosuchians the internal carotid was not enclosed in bone, thus the presence of a carotid foramen is derived for crocodilians.

We discussed the subcapsular process above and we shall not use presence herein. The critical question here might not be the possession of this process but its detailed morphology. This has yet to be determined in non-crocodilians.

Based upon the characters discussed above we would like to offer an improved diagnosis for the Crocodilia based only on cranial characters (these are primitive features for crocodilians):

1. Quadrate akinetic, head is V-shaped with lateral and medial contacts — 'V' points posteriorly. Lateral quadrate contact is with the squamosal, medial contact with the prootic, laterosphenoid, and parietal. Posterior portions of medial and lateral walls of superior temporal fossa are formed by quadrate. Quadrate has numerous lateral "pneumatic" fenestrae.
2. Flat ornamented skull deck, with squamosal arched down behind the otic notch, attaching to the dorsal edge of the paroccipital process along its entire length. Squamosal with lateral smooth shelf for attachment of otic flap.
3. Pneumatic supraoccipital and parietal, with transverse connections between middle ears. Medial and lateral eustachian openings.
4. Broad, sheet-like quadratojugal oriented parasagittally. Primary dorsal contact with postorbital.

5. Fused basiptyergoid articulation.

The Family Protosuchidae

In the last 15 years the number of known protosuchian crocodilians has increased considerably.

Nash (1975) provided a review of protosuchian taxonomy from Broom (1904) through Romer (1972). She rejected attempts to broaden the diagnosis of the Crocodilia (Walker 1970, Romer 1972) and agreed with Bonaparte (1971) that crocodiles are distinct and should not include forms which may only be crocodilian sister groups — specifically, *Sphenosuchus acutus* and related thecodonts. She also rejected (correctly, we feel) the attempts by Walker and Romer to sub-divide the protosuchia at the family level and questioned the validity of assignments of various genera to their proposed families. We accept her conservative classification recognizing a single family (especially since many of the genera are poorly known and are hardly the basis for new families): this is the family Protosuchidae as proposed by Brown (1934). We propose that two subfamilies be recognised: the Protosuchinae, to include all brevirostrine genera normally associated with the Protosuchidae; and the Eopneumatosuchinae, to include the longirostrine *Eopneumatosuchis colberti*, which is distinctly different from all other protosuchians and warrants inclusion in its own separate sub-family. The subfamily Protosuchinae includes those genera listed by Nash (1975): *Pedeticosaurus*, *Notochamps*, *Stegomosuchus*, *Erythrochamps*, *Protosuchus*, *Orthosuchus*, *Platyognathus*, *Hemiprotosuchus*, and possibly *Hoplosuchus*.

DESCRIPTION OF NEW PROTOSUCHIAN

Order Crocodylia Gmelin, 1788

Suborder Protosuchia Mook, 1934

Family Protosuchidae Brown, 1934

Subfamily Protosuchinae Busbey and Gow, 1982

BAROQUEOSUCHUS n. gen.

Etymology.

The name emphasises the ornate architecture of the braincase and quadrate, reminiscent of the baroque period in art and architecture.

Diagnosis. Protosuchian crocodilian with broad flat basicranium meeting occiput at the level of the basisphenoid—basioccipital suture. Internal carotid arteries shielded medially by basisphenoid—basioccipital flanges, unenclosed laterally. Quadrate large and dorsal surface broadly exposed in lateral view.

Distribution, Elliot Formation, Southern Africa.

Type Species. *Baroqueosuchus haughtoni*.

Baroqueosuchus haughtoni n. sp.

Figures 1–12 and Table 1

Etymology

The new species is named in honour of Dr. S.H. Haughton (1888–1982), doyen of South African geology, whose work on the Red Beds published in 1924 set the scene for many important subsequent discoveries.

Holotype. BP-1-4746, partial braincase. Housed in the collections of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.

Type locality. Farm Sunnyside, near Clarens, Orange Free State (O.F.S.), South Africa. Locality co-ordinates 28°31' 40''S; 28°30'06''E (1:50 000 series, map 2828 DA Golden Gate).

Paratype. BP-1-4946., partial braincase with disarticulated squamosals. Housed in the Bernard Price Institute collections, as for the holotype.

Paratype locality. Farm Damplaats near Ladybrand, O.F.S., South Africa. Locality co-ordinates 29°13' 12''S; 27°20'30''E (1:50 000 series, map 2927AB Ladybrand).

Diagnosis. Same as for genus.

DESCRIPTION

The description is based upon the holotype and paratype. The descriptions of the otic bones are primarily based upon the paratype.

BASIOCCIPITAL (Figures 1 and 6). As in modern crocodilians, the basioccipital is a nearly vertical elliptical element lying between the basisphenoid and the foramen magnum that is bordered laterally by the exoccipitals. It contributes the central portion of the occipital condyle. The ventrolateral corners bear small basal tubera. There is a midventral foramen for the passage of the median pharyngotympanic (eustachian) canal and notches for the lateral pharyngotympanic canals ventrolaterally between basioccipital and basisphenoid.

EXOCCIPITAL AND OPISTHOTIC. (Figures 1, 6, 7, 8, 9 and 10). These elements cannot be separated in occipital view but are, unlike those of modern crocodilians, clearly distinguishable in lateral aspect. The lateral extremities of the paroccipital processes are somewhat damaged and distorted. A laterally open cranioquadrate passage runs from a position lateral to the foramen vagi on the occipital surface, up along the anterior face of the paroccipital process. The paroccipital processes are vertical, their ventral margins forming ridges that overhang the openings of the cranioquadrate canals.

Medial to the posterior openings of these canals the exoccipital is pierced by the large, ventrally directed foramen vagi for the passage of nerves IX and X; internally foramina for these nerves pierce the floor of the metotic fissure. The course of the ramus communicans between VII and IX runs down the anterior border of the exoccipital, then turns in under a raised portion of the floor of the metotic fissure towards the internal lateral branch of the foramen vagi, as in modern crocodilians. The exoccipital contributes a very small, lateral portion of the occipital condyle and lateral to this is pierced by a single small foramen for the XIIth nerve. The exoccipital contributes to the roof of the lateral pharyngotympanic canal from where its contact with the basisphenoid runs to the ventrolateral corner of the basicranium; at this point it forms an open channel laterally for the passage of the internal carotid artery. In lateral aspect the course of the cranioquadrate canal is apparent. Dorsally there is a distinct sutural contact of the opisthotic and prootic where these elements border the posterodorsal transverse pneumatic sinus. From here the anterior border of the opisthotic can be traced across the floor of the otic capsule. The subcapsular process is contributed by the opisthotic and overlain anteriorly by an anterodorsal projection of the exoccipital. The median border of the metotic fissure consists of the opisthotic; the posterior wall is pierced dorsally by a foramen communicating with the pneumatic spaces within the opisthotic. The floor of the fissure is pierced by foramina for the IXth and Xth nerves and is raised for the passage beneath it of the ramus communicans. Anterior to the distal portion of the cranioquadrate canal the exoccipital forms a cup shaped recess pierced by a semicircular foramen communicating via a short broad canal with the metotic fissure. The rim of this recess represents the site of the lower quadrate-opisthotic contact in more advanced protosuchians and all other crocodilians. Anteriorly a broad concave surface runs up from the internal border of the lateral pharyngotympanic canal, flanks the ventral pneumatic sinus and terminates in an anterodorsally directed portion hollowed ventrally and pierced posteriorly to transmit the ramus communicans. A groove across the top of the opisthotic marks the course of the occipital vein through a much reduced posttemporal fenestra. Lateral to this there is a distinct facet situated dorsally on the opisthotic for the reception of a lappet of the squamosal.

SUPRAOCCIPITAL. (Figures 1, 6, and 8). The supraoccipital is a triangular bone apparently confined to the occiput by the parietal and just excluded from the border of the foramen magnum by the exoccipital/opisthotic. Vertical median and lateral ridges flanked by depressions constitute the site of attachment of neck muscles (*M. spinalis capitis*). The suture with the parietal appears to run in a groove above the lateral ridges and through the central ridge beneath a posteriorly directed pointed extension of the parietal. In lateral aspect the reg-



Figure 1. *Baroqueosuchus haughtoni* BP-1-4946.
Stereophotographs of (from top to bottom):—
Occiput.
Skull roof with squamosals removed.
Skull roof with squamosals in position.
Ventral surface of left squamosal.
Scale = 1 cm

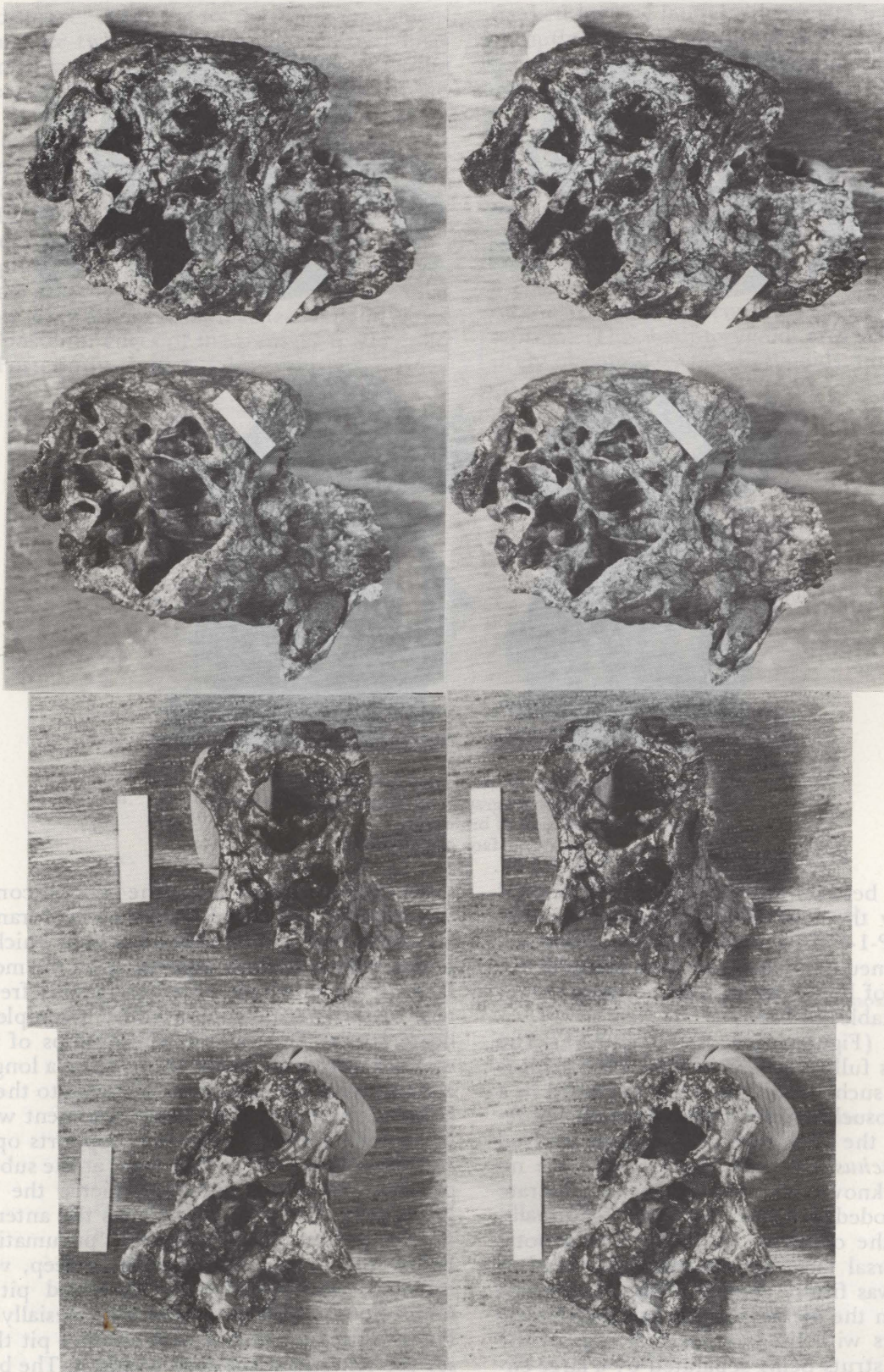


Figure 2. *Baroqueosuchus haughtoni* BP-1-4946.

Stereophotographs of (from top to bottom):—

Right side of braincase with quadrate in position.

Right side of braincase with quadrate removed.

Dorsal surface of right quadrate.

Ventral surface of right quadrate.

Scale = 1 cm.

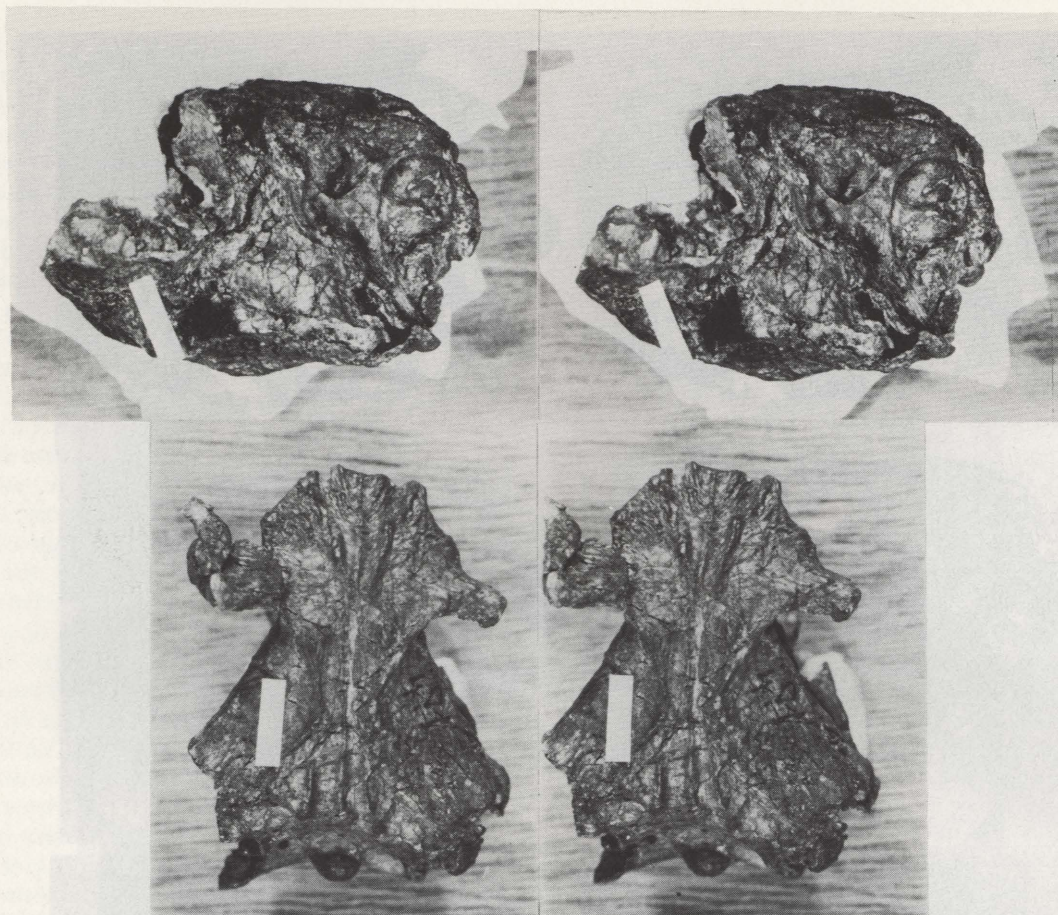


Figure 3. *Baroqueosuchus haughtoni* BP-1-4946.
Stereophotographs of (from top to bottom):—
Left side of braincase.
Ventral surface of braincase.
Scale = 1 cm.

ion of overlap between parietal and supraoccipital is obscured by the foot of a buttress of prootic. Breakage in BP-1-4746 shows that the supraoccipital was fully pneumatic as in modern crocodilians; small spicules of bone can be seen between the inner and outer tables of bone.

PROOTIC. (Figures 2, 4, 8, 10, and 11). The right prootic is fully exposed in BP-1-4946. This is the first time such detail has been displayed in a primitive protosuchian crocodilian (not all the relationships of the braincase of the more derived *Eopneumatosuchus* are fully understood since no quadrates are known and the regions of quadrate contact are eroded) because this bone is normally obscured by the overlying quadrate. The prootic has a large dorsal facet against which the head of the quadrate was firmly applied. This is buttressed fore and aft on the mesial surface by struts having robust contacts with the lateroventral edge of the parietal, these struts being separated by a large circular opening for the anterior transverse pneumatic canal. The posterior strut is pierced by a foramen that transmitted the occipital vein. This strut partially overlies the supraoccipital and abuts against the opisthotic. Antero-dorsally the prootic contacts the parietal and laterosphenoid. The region behind the anterior transverse pneumatic sinus is a complex of struts and foramina (for which func-

tions cannot be assigned). The prootic contributes the anterior and dorsal border of the foramen ovale, where it is formed into a low boss which corresponds with a shallow depression on the mesial surface of the quadrate; this boss stands free of the wall of the prootic supported by a complex of delicate struts. The ventral relationships of the prootic are not clear. There seems to be a long sutural contact with the basisphenoid dorsal to the carotid pillar of the latter and clearly confluent with it. A prominent cochlear eminence supports opisthotic and exoccipital where they meet at the subcapsular process. Numerous foramina pierce the prootic. Posteriorly the bone contributes the anterior wall of the posterodorsal transverse pneumatic sinus. Below this is the otic capsule, a deep, vertically oriented, anteroposteriorly elongated pit with a bony floor which communicates mesially via the fenestra pseudorotunda with another pit that houses the fenestra ovalis deep within it. The bony rim surrounding the fenestra ovalis is pierced anterodorsally by a small foramen from whence a groove runs along the anterior rim. Anterior to the ear region is a small foramen for the transmission of the VIIth nerve. Running ventrally from this the course of palatine branch of VII has left its impression in the surface of the bone, while a dorsal impression marks the course of the hyomandibular branch for

a short distance. Anterior to the transverse pneumatic sinus are two foramina connected by a marked depression on the surface of the prootic; the dorsal foramen has the form of a narrow slit, so that this is probably the course of a nerve rather than a blood vessel. Below the dorsal quadrate articulation of the prootic lies a group of three foramina linked to the pneumatic sinus within.

BASISPHENOID. (Figures 3, 5, 6, 7 and 8). The bone is exposed as a broad plate on the ventral and occipital surfaces. Sutures with the pterygoids are distinct on the ventral surface where a medial projection of basisphenoid reaches a point level with the posterior edges of the transverse pterygoid flanges. Posteriorly there is a low midventral ridge

flanked by low lateral ridges. The bone sweeps up abruptly onto the occipital surface where it meets the exoccipitals and basioccipital. The basisphenoid has a ventrolateral contact with the quadrate. Detailed outlines of the basisphenoid rostrum are difficult to interpret due to cracking and distortion. The pila antotica is firmly sutured to the laterosphenoid. Foramina emerging laterally from the region of the hypophysial fossa transmitted the internal carotid artery above and the VIth nerve below. The rostrum is enveloped below by the pterygoids which rise anteriorly to the full height of the rostrum and continue forward as a median septum. The basiptyergoid articulations are entirely obscured by the pterygoids. Internally, in the

Abbreviations

Bo	basioccipital
Bs	basisphenoid
b.t.	basal tubera
c.Q.c.	cranioquadrate canal
d.l.Q.	dorsal lappet of quadrate
d.t.p.s.	dorsal transverse pneumatic sinus
Ect	ectopterygoid
e.f.g.	ear flap groove
Eo	exoccipital
f.o.	foramen ovale
fen. o	fenestra ovalis
f.p.r.	fenestra pseudorotundum
i.c.a.	internal carotid artery
L	laterosphenoid
l.p.c.	lateral pharyngotympanic canal
m.f.	metotic fissure
m.p.c.	median pharyngotympanic canal
o.c.	occipital condyle
Op	opisthotic
Op a.Sq	opisthotic articulation for squamosal
o.v.	occipital vein
P	parietal
Pal	palatine
P.a.Q	prootic articulation for quadrate
poc.r.	postcarotid recess
prc.r.	precarotid recess
Pt	pterygoid
Ptf	pterygoid flange
p.t.f.	post temporal fenestra
Q	quadrate
r.c.	ramus communicans
r.io.v.	rim of infraorbital vacuity
ro.Bs	basisphenoid rostrum
r.s.	rhomboid sinus
s.c.p.	subcapsular process
So	supraoccipital
Sq	squamosal
v.l.Q	ventral lappet of quadrate
v.p.s.	ventral pneumatic sinus

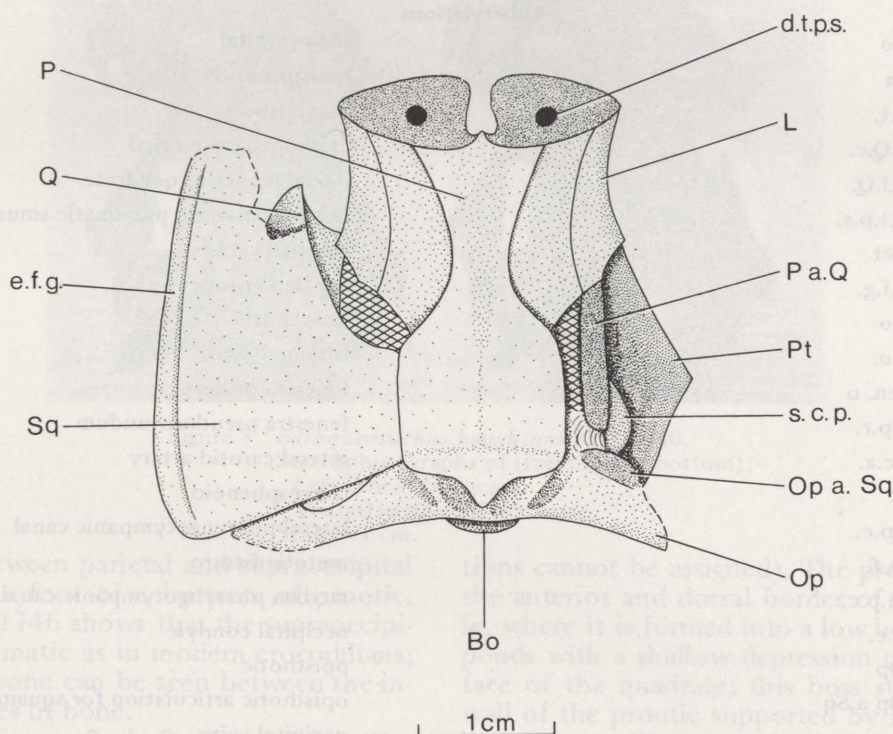


Figure 4. *Baroqueosuchus haughtoni*.
Dorsal view of BP-1-4746 (above) and BP-1-4946 (below).

region occupied by the basisphenoidal pneumatic sinuses, the basisphenoid consists of a delicate filigree of interconnecting struts.

LATEROSPHEOID. (Figures 4, 8 and 9). The laterosphenoid has a straight nearly horizontal sutural contact with the parietal just above the level of the upper contact between prootic and quadrate. In both specimens the delicate postorbital processes of the laterosphenoids are damaged, but are present as delicate lateral flanges directed out towards the postorbital bar. The bone contributes the pillar anterior to the foramen ovale and meets the basisphenoid below this where the contact is obscured by a sheet of the pterygoid reaching to the same height. The posterior edge of the laterosphenoid, as far as the top of the foramen ovale, is overlapped slightly by the quadrate. Laterally the bone is separated by a rounded ridge into temporal and orbital surfaces. The laterosphenoids meet in the dorsal

midline, though there is some damage in this area. These bones are exposed dorsally anterior to the parietal where each is pierced by a dorsally facing foramen for the passage of the anterior transverse pneumatic sinus; the area between them housed the olfactory lobe of the brain. The ventral orbital surface of the laterosphenoid contains several foramina and received the pila antotica of the basisphenoid. V3 emerges medial to the pillar in front of the foramen ovale. Medial to this is a smaller foramen for the levator bulbi branch of V. Above these latter foramina is the tiny exit of IV. The anterior edge of the laterosphenoid bears two indentations marking the points of exit of nerves II and III.

PARIETAL. (Figures 1, 4, 6, 7 and 8). The single fused parietal has a pitted dorsal surface. A slight ridge separates dorsal and temporal parts of the parietal anteriorly and becomes a deep recess poster-

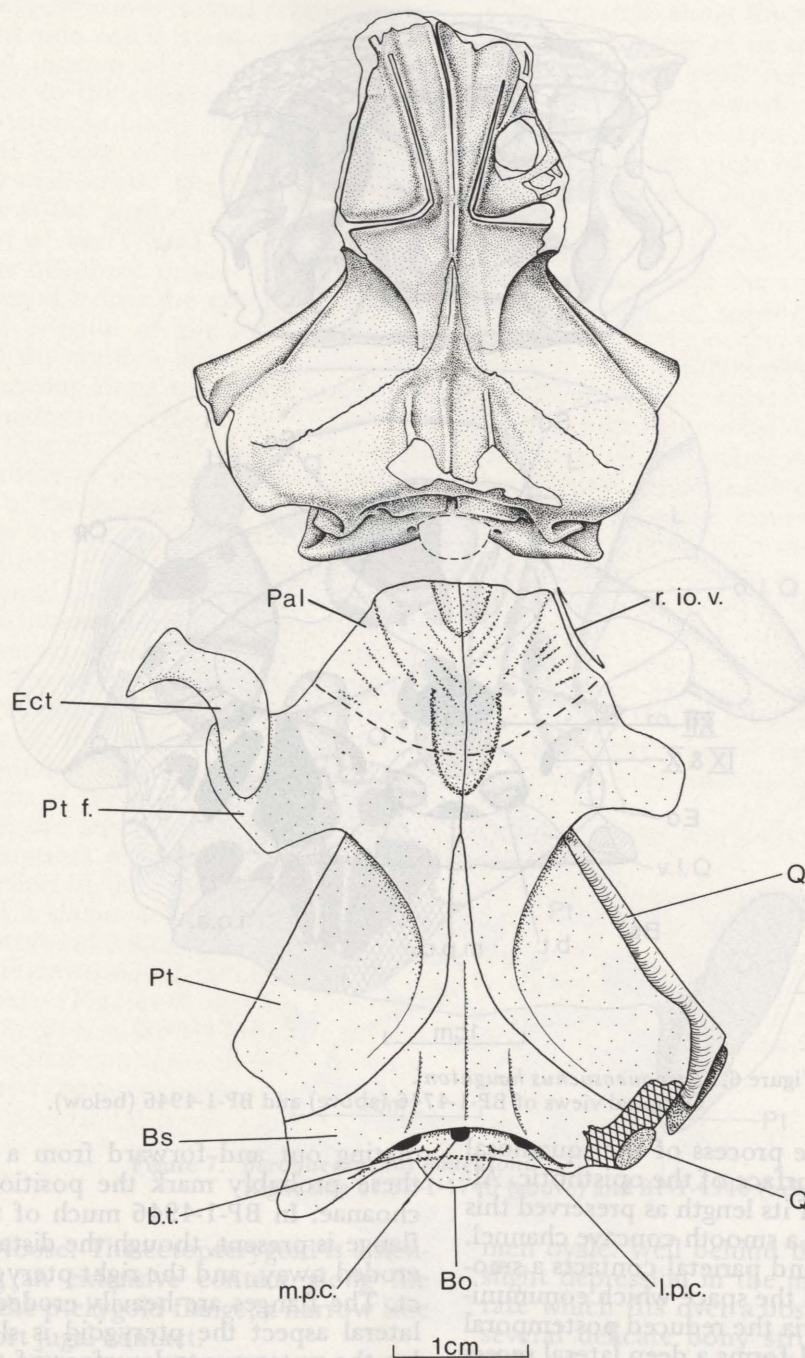


Figure 5. *Baroqueosuchus haughtoni*.
Ventral view of BP-1-4746 (above and BP-1-4946 (below).

iorly. The anterior edge of the parietal bears a small median raised 'nib' with grooves lateral to it for the reception of the frontals. The contact with the supraoccipital is at the top of the occiput, from whence the supraoccipital runs under the parietal. Sutures with the squamosals are slightly concave. The sutural contacts with the prootic and laterosphenoid are described above.

SQUAMOSAL. (Figures 4, 6, 7 and 10). The disarticulated squamosals of BP-1-4946 allow a complete description of their contacts. The squamosal has an ornamentation of grooves and pits, with long grooves near the attachment site for the

ear flaps. The ledge for the ear flap can be traced along its lateral edge. Most of the facet which contacts the parietal is preserved, as also is part of the lateral and posterior border of the upper temporal fenestra. Posteriorly there is a wide groove for the attachment of neck musculature. Below this is a facet with a rounded distal edge, occupying the proximal two thirds of the width, for the reception of the paroccipital process of the opisthotic. A small raised flap of bone near its base rests on a facet of the dorsal surface of the opisthotic. On the ventral surface the attachment for the quadrate runs from the outer rim of the upper temporal opening

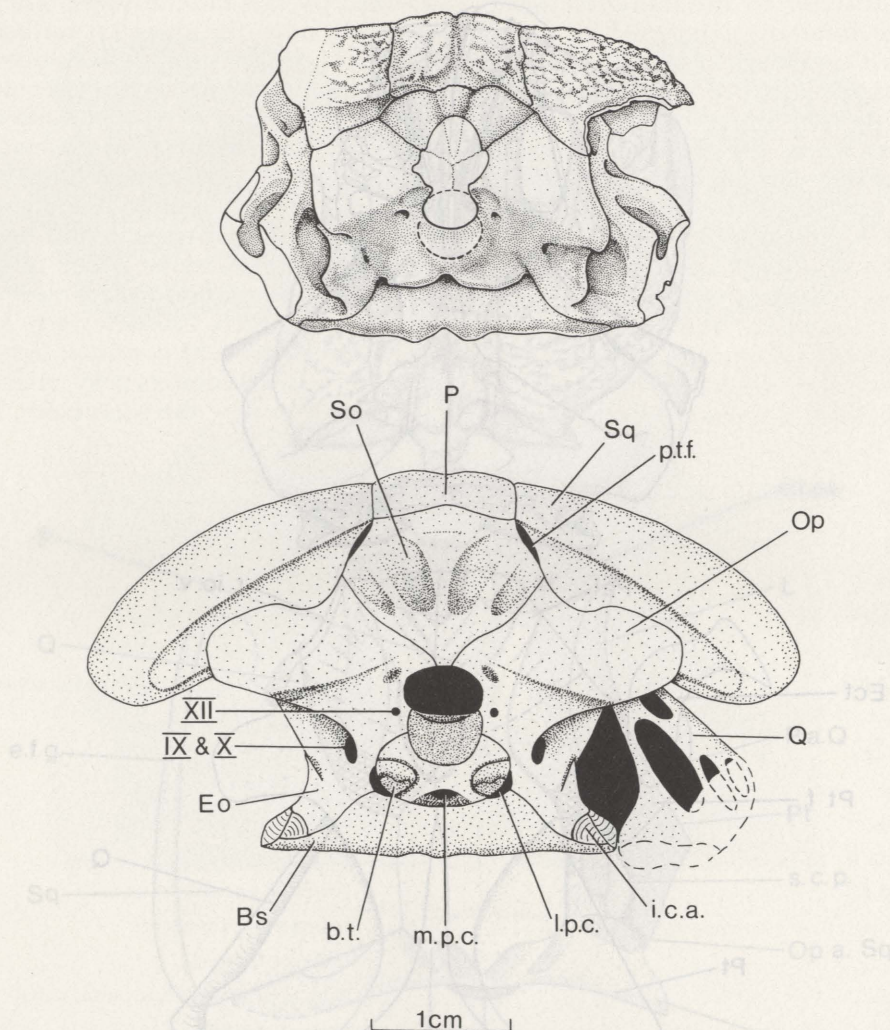


Figure 6. *Baroqueosuchus haughtoni*.
Occipital views of BP-1-4746 (above) and BP-1-4946 (below).

back to abut against the process of the squamosal that lies on the dorsal surface of the opisthotic. Along the posterior half of its length as preserved this contact has the form of a smooth concave channel. Between the quadrate and parietal contacts a smooth surface region roofs the space which communicates with the occiput via the reduced posttemporal fenestra. The squamosal forms a deep lateral recess covering the ear region.

QUADRATOJUGAL. The quadratojugals are absent from both specimens. The broad dorso-lateral edge of the postorbital bar indicates that the quadratojugal was a thin broad sheet oriented parasagittally, as in *Hemiprotosuchus*. The primary contact of the quadratojugal seems to have been with the postorbital bar.

PALATINES. Portions of the palatines may be present but, as no sutures are discernible on either specimen, they will be treated with the pterygoids.

PTERYGOIDS. (Figures 3, 5, 7, and 9). The relationship of the pterygoids to the basisphenoid in ventral view is shown in the illustrations.

From the point where the pterygoids meet in the midline the surface is marked by several ridges ra-

diating out and forward from a midventral ridge; these probably mark the position of the internal choanae. In BP-1-4946 much of the left pterygoid flange is present, though the distal surface has been eroded away, and the right pterygoid flange is intact. The flanges are heavily eroded in BP-1-4746. In lateral aspect the pterygoid is slightly overlapped by the anteroventral surface of the quadrate. The pterygoid rises to the level of the basisphenoid/laterosphenoid contact, then dips anteriorly exposing much of the basisphenoid rostrum. The pterygoids then meet to form a vertical septum which enfolds the anterior portion of the rostrum. The quadrate ramus of the pterygoid consists of a thin sheet in rigid overlapping contact with the basisphenoid ventrally; it curves up onto the ventrolateral surface of the braincase where it is overlapped anteriorly by the ventral quadrate lappet. The internal contact with the pterygoid ramus of the quadrate is not displayed in either specimen.

ECTOPTYERYGOID. (Figures 5 and 7). The left ectopterygoid of BP-1-4946 was preserved intact lying on the dorsal surface of the root of the pterygoid flange. The proximal portion of the right ele-

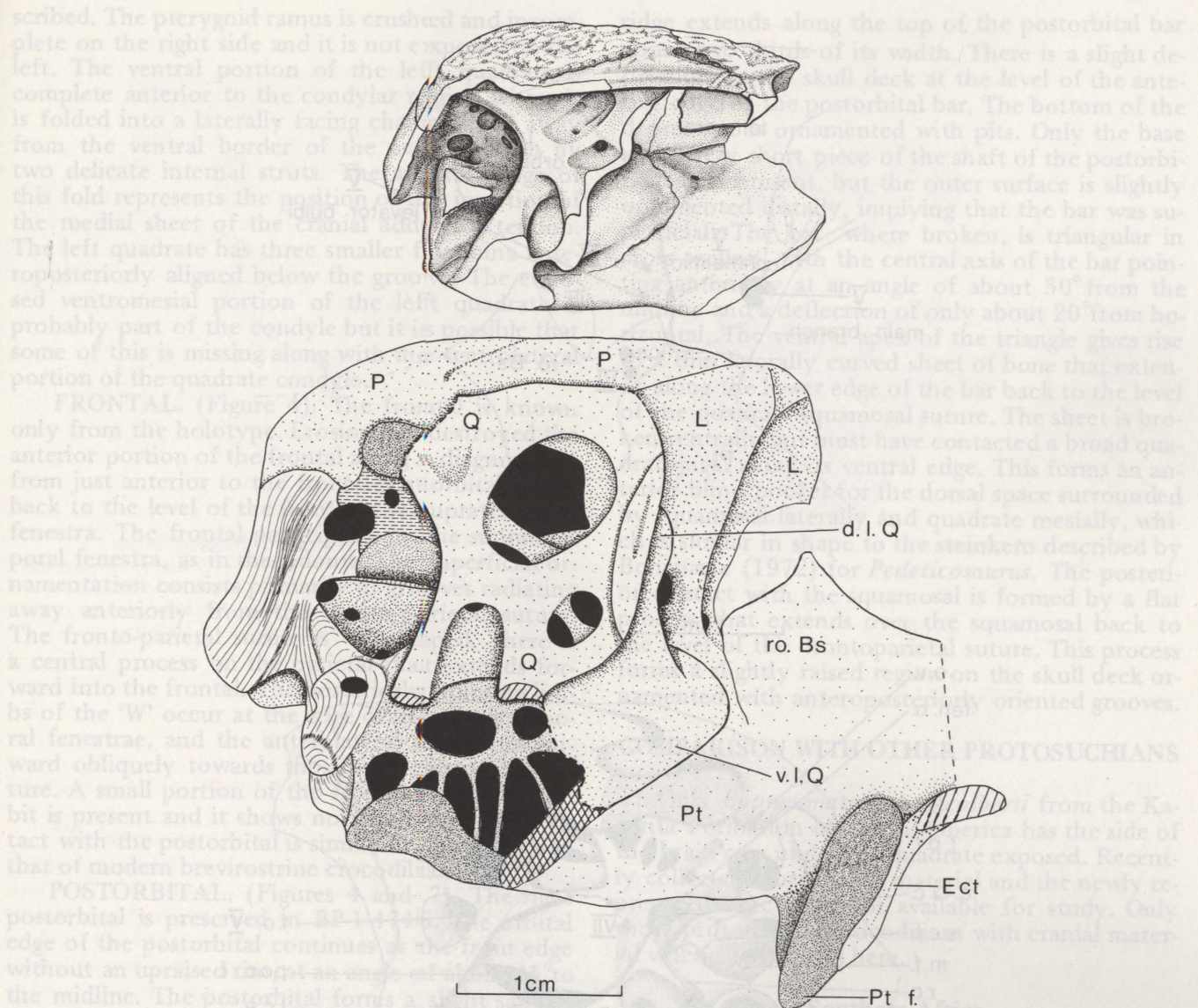


Figure 7. *Baroqueosuchus haughtoni*.
Right side of BP-1-4746 (above) and BP-1-4946 (below).

ment was found loose. The ectopterygoid is a slender bone having an extensive contact along the anterior edge of the pterygoid flange, a narrow free portion and a short jugal contact.

QUADRATE. (Figures 6, 7 and 9). The quadrates were better revealed in BP-1-4946 because of the removal of one, and the description below will specifically refer to that specimen. The left quadrate is the more complete, lacking only most of the articulatory condyle. This quadrate is somewhat distorted which makes precise reconstruction and comparison with the right quadrate, itself probably distorted, difficult. The quadrates were easily distorted because they are thin and delicate. Both bones are illustrated as preserved. The quadrate has extensive contacts with the side wall of the braincase. Mesial contacts are with the prootic, laterosphenoid and parietal above, and basisphenoid below. Anteriorly two delicate sigmoid lappets of the quadrate overlap several bones. The dorsal lappet lies on laterosphenoid and partially walls the fora-

men ovale. Well behind the edge of this lappet is a slight depression in the mesial surface of the quadrate which fits over a boss of prootic supported by several delicate bony struts. The lower lappet lies along the most superficial of these structures, extending onto the laterosphenoid and pterygoid. Between these lappets and the anterolateral border of the quadrate is a smooth notch forming the posterior border of the dorsal portion of the temporal fossa. The dorsal two thirds at least of this anterior border of the quadrate lateral surface presents a broad grooved area for contact with the quadratojugal. More ventrally the border narrows so that one cannot be certain of the full extent of the quadratojugal contact. The posterior edge of the quadrate forms a posteriorly concave otic notch. This edge nowhere contacts the braincase or squamosal so that the cranioquadrate canal and otic region are exposed laterally and do not form a closed otic meatus posteriorly. The quadrate is pierced by several large foramina the most prominent of which

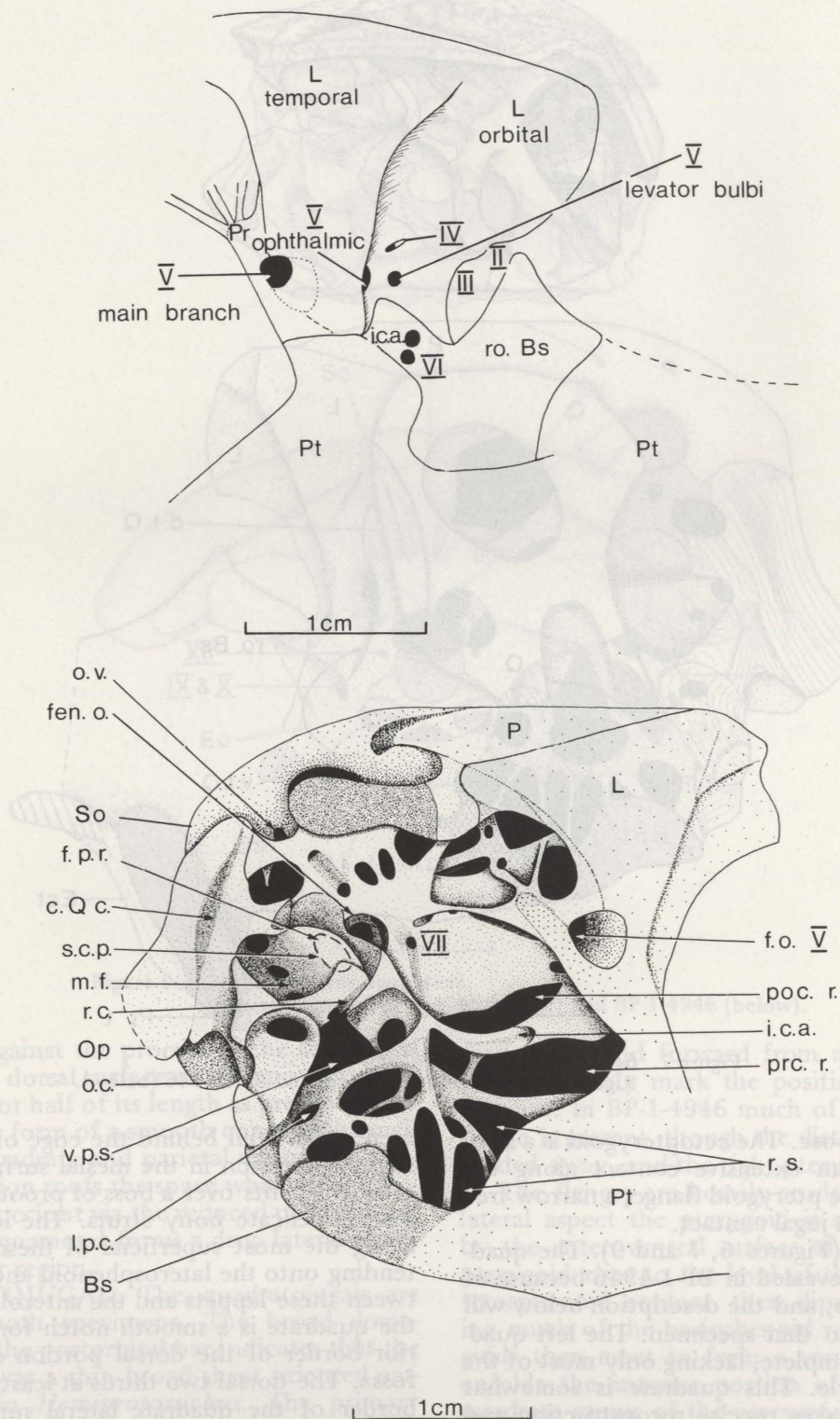


Figure 8. *Baroqueosuchus haughtoni*.
Right side of BP-14946.

Above: Anterior oblique view showing anterior cranial nerve exits.

Below: Braincase detail.

is situated middorsally. Within it a rim of bone forms a deep pocket anteriorly; there are short ventral struts supporting an anteroposteriorly arranged brace continuous with the top of the ventral lappet. Below and anterior to this foramen is a smaller one bisected by a deep strut of bone. Behind this is a

large, dorsoventrally oriented groove floored in the dorsal portion by part of the pterygoid ramus of the quadrate. The top of the groove is pierced by a small foramen which emerges in the prominent oval depression on the mesial surface, that communicates with the other foramen previously de-

scribed. The pterygoid ramus is crushed and incomplete on the right side and it is not exposed on the left. The ventral portion of the left quadrate is complete anterior to the condylar region where it is folded into a laterally facing channel held away from the ventral border of the oval foramen by two delicate internal struts. The anterior edge of this fold represents the position of the insertion of the medial sheet of the cranial adductor tendon. The left quadrate has three smaller foramina anteroposteriorly aligned below the groove. The exposed ventromesial portion of the left quadrate is probably part of the condyle but it is possible that some of this is missing along with the ventrolateral portion of the quadrate condyle.

FRONTAL. (Figure 4). The frontal is known only from the holotype. Erosion has destroyed the anterior portion of the frontal along a diagonal line from just anterior to the frontal-postorbital suture back to the level of the front of the supratemporal fenestra. The frontal participates in the supratemporal fenestra, as in thecodonts. The superficial ornamentation consists primarily of grooves radiating away anteriorly from the fronto-parietal suture. The fronto-parietal suture is 'W'-shaped. There is a central process on the parietal that extends forward into the frontal. The posteriorly pointing limbs of the 'W' occur at the edge of the supratemporal fenestrae, and the anterolateral limbs run forward obliquely towards the frontal-postorbital suture. A small portion of the frontal rim of the orbit is present and it shows no raised rim. The contact with the postorbital is similar in appearance to that of modern brevirostrine crocodilians.

POSTORBITAL. (Figures 4 and 7). The right postorbital is preserved in BP-1-4746. The orbital edge of the postorbital continues as the front edge without an upraised rim, at an angle of about 45° to the midline. The postorbital forms a slight saddle-shaped surface into which the frontal inserts, with a long process extending under the frontal. A slight

ridge extends along the top of the postorbital bar about two thirds of its width. There is a slight depression on the skull deck at the level of the anterior edge of the postorbital bar. The bottom of the depression is ornamented with pits. Only the base and a very short piece of the shaft of the postorbital bar is present, but the outer surface is slightly ornamented distally, implying that the bar was superficial. The bar where broken, is triangular in cross section, with the central axis of the bar pointing anteriorly at an angle of about 30° from the midline and a deflection of only about 20° from horizontal. The ventral apex of the triangle gives rise to a thin laterally curved sheet of bone that extends along the lower edge of the bar back to the level of the quadrate-squamosal suture. The sheet is broken ventrally but must have contacted a broad quadratojugal along its ventral edge. This forms an anterior blind pocket for the dorsal space surrounded by squamosal laterally and quadrate mesially, which is similar in shape to the steinkern described by Bonaparte (1972) for *Pedeticosaurus*. The posterior contact with the squamosal is formed by a flat process that extends over the squamosal back to the level of the frontoparietal suture. This process forms a slightly raised region on the skull deck ornamented with anteroposteriorly oriented grooves.

COMPARISON WITH OTHER PROTOSUCHIANS

Only *Eopneumatosuchus colberti* from the Kayenta Formation of North America has the side of the brain case under the quadrate exposed. Recently collected *Protosuchus* material and the newly re-prepared type were not available for study. Only those protosuchian crocodilians with cranial material will be considered here.

Southern Africa

Nash (1975) presents a summary of the taxon-

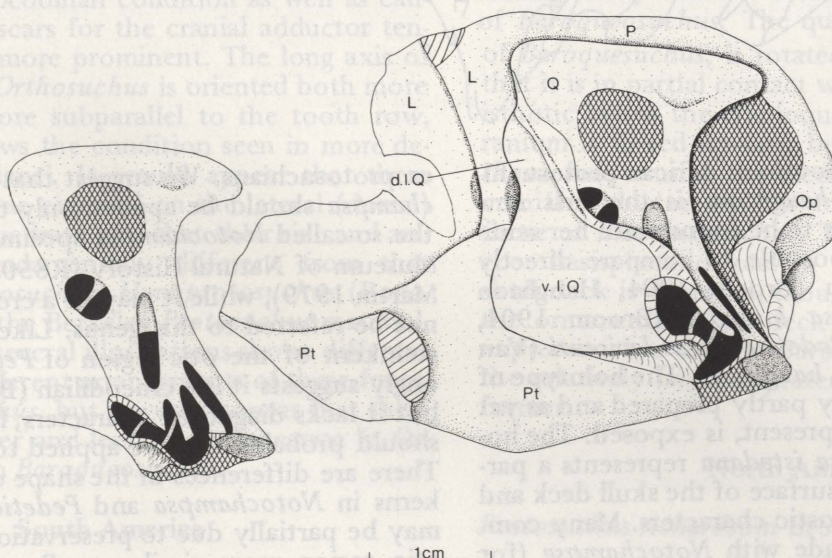


Figure 9. *Baroqueosuchus haughtoni*, BP-1-4946
Left side of braincase and posterior oblique aspect of dorsal surface of left quadrate.

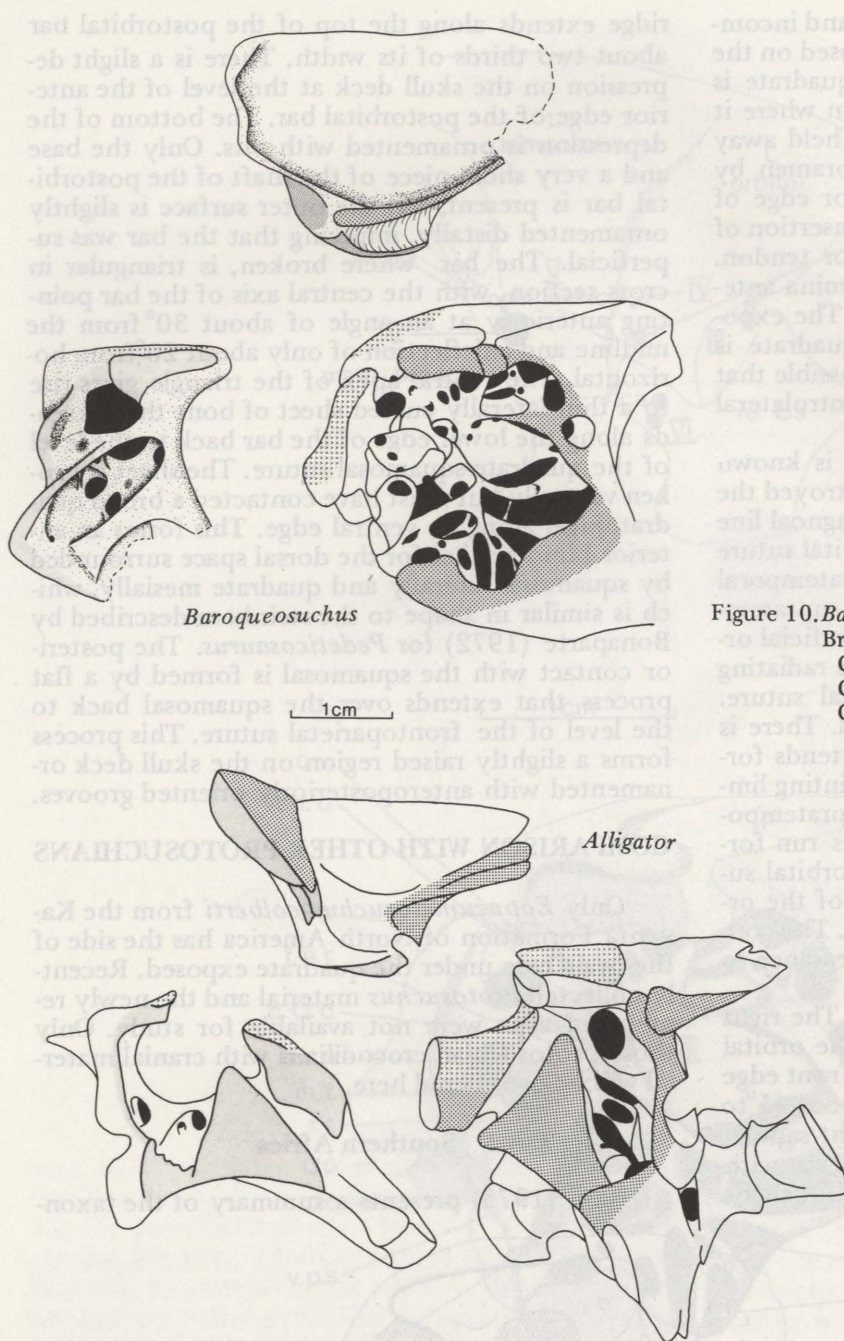


Figure 10. *Baroqueosuchus* above. *Alligator* below.
Braincase with prootic and squamosal folded out.
Contacts for prootic — heavy stipple.
Contacts for braincase — light stipple.
Contacts for squamosal — V. pattern.

omy and localities of Southern African protosuchians; *Baroqueosuchus haughtoni* is the first new southern African genus to be found since her seminal paper. It is not possible to compare directly *Notochampsia istedana* (Broom 1904, Haughton 1924), *Erythrochampsia longipes* (Broom 1904, Haughton 1924), or *Pedeticosaurus levisi* (Van Hoepen 1915) with *B. haughtoni*. The holotype of *Erythrochampsia* is only partly prepared and as yet no cranial material, if present, is exposed. The holotype of *Notochampsia istedana* represents a partial mold of the undersurface of the skull deck and does not exhibit diagnostic characters. Many comparisons have been made with *Notochampsia* (for example see Nash 1975), but since this specimen is a steinkern the dorsal surface and so-called sutures are not directly comparable to dorsal views of oth-

er protosuchians. We suggest that the name *Notochampsia* should be applied only to the type; thus the so-called *Notochampsia* specimen at the British Museum of Natural History (R8503) (Whetstone & Martin 1979), while it may be a crocodilian, should not be referred to this genus. Likewise, the partial steinkern of the otic region of *Pedeticosaurus* strongly suggests it is a crocodilian (Bonaparte 1972), but it lacks diagnostic characters; hence, this name should probably also be applied to the type only. There are differences in the shape of the otic steinkerns in *Notochampsia* and *Pedeticosaurus*, which may be partially due to preservation. Both have an otic region more similar to *Baroqueosuchus* than *Orthosuchus*.

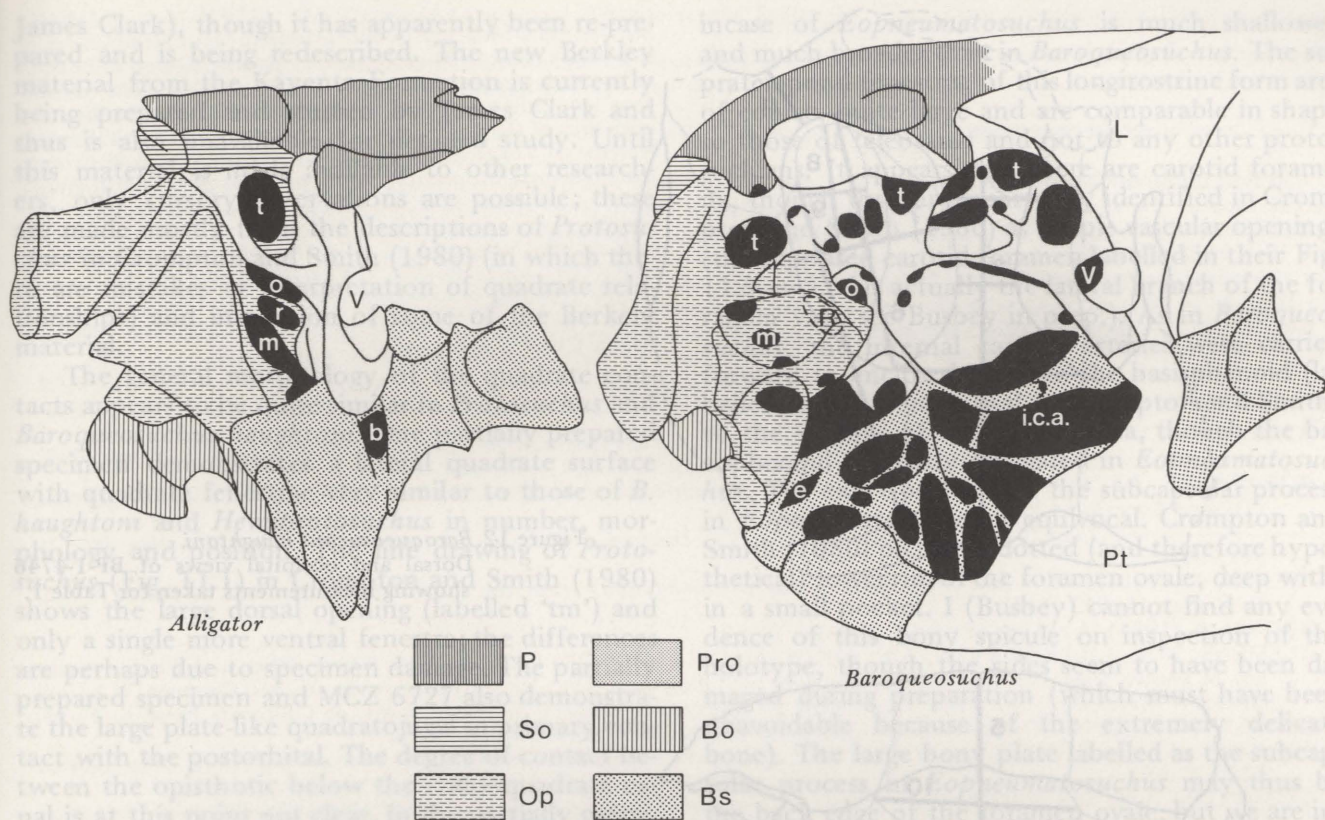


Figure 11. Braincase of *Baroqueosuchus* and *Alligator* compared.

Orthosuchus stormbergi (Nash 1968, 1975).

The braincase of both the type and paratype of *Baroqueosuchus* is larger, deeper, and broader than that of *Orthosuchus*. *Orthosuchus* demonstrates two major features that are derived over *Baroqueosuchus*: the internal carotids are enclosed in carotid foramina and the opisthotic and quadrate are in contact below the cranioquadrate canal. In addition, the entire basicranium is flexed up at the back edge of the pterygoid flanges, producing a more characteristic crocodilian condition as well as causing the medial scars for the cranial adductor tendon to become more prominent. The long axis of the quadrate of *Orthosuchus* is oriented both more medially and more subparallel to the tooth row, which foreshadows the condition seen in more derived 'mesosuchians'. It would appear that there are fewer fenestrae exposed on the lateral (dorsal) surface of the quadrate and that their size and arrangement is fundamentally different from that seen in *Baroqueosuchus*, *Hemiprotosuchus* (Bonaparte 1971), or the Berkeley *Protosuchus* material. Nash (1975) in several illustrations shows different numbers and different arrangements of these fenestrae in *Orthosuchus*, but it would appear that there are actually fewer and less ornate fenestrae in *Orthosuchus* than in *Baroqueosuchus*.

South America

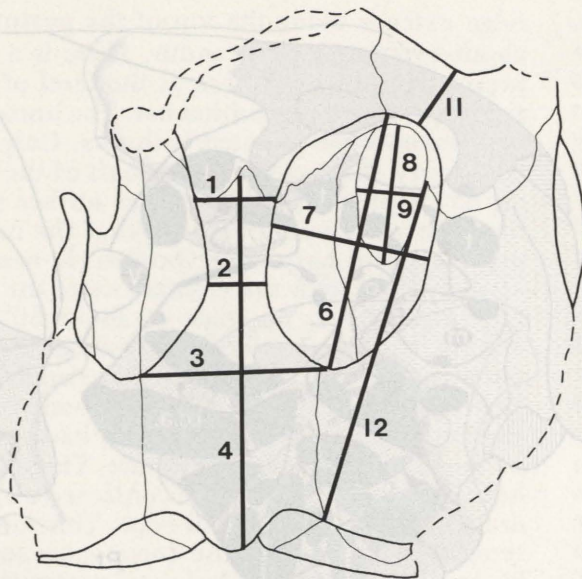
Hemiprotosuchus leali (Bonaparte 1971) is the only protosuchian known from South America. The holotype and paratype material are from the

upper Triassic Los Colarados Formation of La Rioja, Argentina. The type material represents a smaller animal than *Baroqueosuchus*. The number and arrangement of lateral quadrate fenestrae appear to be quite similar to those of *Baroqueosuchus* which in fact compare favourably with those seen in *Protosuchus* (based on the unpublished Berkeley material). It should be noted that the position of the tympanum, the attachments of the quadrate to the skull, and the occiput are incorrectly restored in Bonaparte's original description (Busbey, in prep.); suffice to say that the otic region is similar to that of *Baroqueosuchus*. The quadrate, relative to that of *Baroqueosuchus*, is rotated further to the rear so that it is in partial contact with the body of the opisthotic below the cranioquadrate canal. The basicranium is flexed upward, but not as much as in *Orthosuchus*, causing the medial tendon ridges of the cranial adductor tendon to be more robust than those of *Baroqueosuchus*. This also results in a deeper basisphenoid keel in *Hemiprotosuchus*. The skull deck is damaged, though it would appear that the ornamented skull deck is less extensive in *Hemiprotosuchus* than in *Baroqueosuchus* because of the relatively larger supratemporal fenestrae of the former.

North America

Protosuchus richardsoni Brown (1933)

The holotype of *Protosuchus richardsoni* (Brown 1933, Colbert and Mook 1951) is currently unavailable for study (Max Hecht pers. comm. to

Figure 12. *Baroqueosuchus haughtoni*.

Dorsal and occipital views of BP-1-4746 showing measurements taken for Table 1.

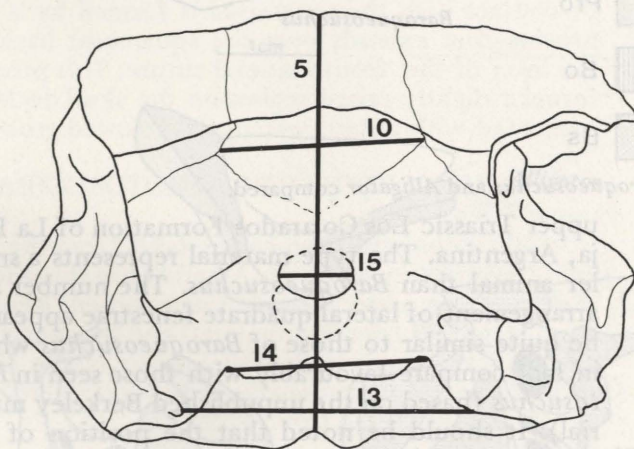


Table 1 : Measurements of type skulls (in mm.).

	BP-1 4746	BP-1 4946
1. Width of skull table at fronto-parietal suture	6,6	7,0
2. Minimum width skull table	3,6	3,8
3. Width of skull table at posterior edge of supratemporal fenestra	13,2	12,9
4. Length of parietal	28,3	26,2
5. Height of skull	35,7	34,4
6. External length supratemporal fenestra	21,6	—
7. External width supratemporal fenestra	11,7	12,2
8. Internal length supratemporal fenestra	12,2	—
9. Internal width supratemporal fenestra	4,7	4,6
10. Maximum width of supraoccipital (at posttemporal fenestrae)	13,2	13,1
11. Minimum width of postorbital behind orbit	6,6	—
12. Length of head of quadrate at squamosal suture	26,0	23,0
13. Width across basicranium (at level of carotid notches)	24,8	19,0
14. Width across basicranium (at lateral pharyngotympanic openings)	16,0	12,6
15. Width foramen magnum	6,5	6,3

James Clark), though it has apparently been re-prepared and is being redescribed. The new Berkley material from the Kayenta Formation is currently being prepared and studied by James Clark and thus is also unavailable for detailed study. Until this material is made available to other researchers, only cursory observations are possible; these are made mostly from the descriptions of *Protosuchus* in Crompton and Smith (1980) (in which there are mistakes in interpretation of quadrate relationships) and inspection of some of the Berkely material.

The general morphology of the quadrate contacts appears to be quite similar in *Protosuchus* and *Baroqueosuchus haughtoni*. One partially prepared specimen demonstrates a lateral quadrate surface with quadrate fenestrae very similar to those of *B. haughtoni* and *Hemiprotosuchus* in number, morphology and position. The line drawing of *Protosuchus* (Fig. 11.1) in Crompton and Smith (1980) shows the large dorsal opening (labelled 'tm') and only a single more ventral fenestra; the differences are perhaps due to specimen damage. The partially prepared specimen and MCZ 6727 also demonstrate the large plate-like quadratojugal in primary contact with the postorbital. The degree of contact between the opisthotic below the cranioquadrate canal is at this point not clear. In the partially prepared specimen the lower edges of the quadrate and body of the opisthotic are not exposed, but at least two thirds of the body of the opisthotic is not in contact with the quadrate. In other, more badly crushed Berkely material, it would appear that the quadrate and opisthotic are in slight contact ventrally but this could be due to crushing. In any case, the physical separation of the quadrate and opisthotic in *Protosuchus* and *Baroqueosuchus* seems to be greater than in *Hemiprotosuchus* and as such they represent less derived animals. The basicranium of *Protosuchus* is, as in *Hemiprotosuchus*, flexed up at the back and as a result has the more robust basisphenoid keel and medial cranial adductor tendon scars. The supratemporal fossae of *Protosuchus* are relatively smaller than those of *Baroqueosuchus* (based on the restoration in Crompton and Smith (1980) and Colbert and Mook (1951) and are essentially 'juvenile' in shape and orientation. This results in a very broad skull deck lateral to the supratemporal fenestra and between the supratemporal fenestrae, unlike *Baroqueosuchus*.

Eopneumatosuchus colberti Crompton and Smith (1980).

Eopneumatosuchus is the first longirostrine protosuchian crocodilian that has been found. Because of this the bones of the braincase are rather expanded anteriorly, quite unlike *Baroqueosuchus*. Unfortunately the quadrates and regions of quadrate contact on the braincase proper are eroded and thus do not preserve any evidence of an opisthotic-quadrate contact below the cranioquadrate canal (contra Crompton and Smith 1980). The bra-

in case of *Eopneumatosuchus* is much shallower and much broader than in *Baroqueosuchus*. The supratemporal fenestrae of this longirostrine form are, of course, quite large and are comparable in shape to those of teleosaurs and not to any other protosuchians. It appears that there are carotid foramina, though they are incorrectly identified in Crompton and Smith (1980) as simple vascular openings (the supposed carotid foramen labelled in their Fig. 11.3 as 'i.c.' is actually the lateral branch of the foramen vagi, see Busbey in prep.). As in *Baroqueosuchus*, the internal carotid arteries were carried forward in enclosed tubes in the basisphenoid (labelled as the vidian canal in Crompton and Smith) to the vicinity of the sella turcica, though the basisphenoid is greatly elongated in *Eopneumatosuchus*. The exact position of the subcapsular process in *Eopneumatosuchus* is equivocal. Crompton and Smith (1980) picture a dotted (and therefore hypothetical) lower rim of the foramen ovale, deep within a small pocket. I (Busbey) cannot find any evidence of this bony spicule on inspection of the holotype, though the sides seem to have been damaged during preparation (which must have been unavoidable because of the extremely delicate bone). The large bony plate labelled as the subcapsular process in *Eopneumatosuchus* may thus be the back edge of the foramen ovale, but we are inclined to accept Crompton and Smith's (1980) interpretation based upon general size and position of the large process. A similar large plate in *Baroqueosuchus* is similarly interpreted as being the subcapsular process; the delicate bony lower edge of the foramen ovale is preserved. Both *Baroqueosuchus* and *Eopneumatosuchus* demonstrate a remarkable degree of pneumaticity, especially in the basisphenoid. This is assumed to be primitive for crocodilians, and represents the morphology of the basisphenoid before its anteroposterior shortening and flexure in the region of the opening of the medial pharyngotympanic canal. *Eopneumatosuchus* does have greater pneumaticity than *Baroqueosuchus*, due to the anterior and lateral expansion of the bones of the braincase and skull roof.

PROTOSUCHIAN RELATIONSHIPS

The known protosuchian crocodilians occur within a fairly narrow time span, probably no earlier than Rhaetian to no later than Late Liassic. Nevertheless, they demonstrate a fairly rapid change from the condition of *Baroqueosuchus* which we consider to be the most primitive crocodilian, to that of *Orthosuchus* where the quadrate has rotated up to contact the opisthotic and form a rather 'modern' basicranium. With the preparation of the new Berkeley material the similarities between *Baroqueosuchus* and *Protosuchus* are quite evident, mainly the orientation, relationships and fenestrae of the quadrate. The only southern African forms which seem to have the right sizes and shapes to be related to *Baroqueosuchus* are not sufficiently well preserved to find important diagnostic

characters. *Orthosuchus stormbergi* is dissimilar to *Baroqueosuchus* in its size, proportions, and details of sutural contacts.

ACKNOWLEDGEMENTS

Travel funds to South Africa for the first author and partial support for illustrations were made possible by National Science Foundation Research Grants DEB 77-25339 and DEB 80-22183 to Dr. James A. Hopson. The first author also wishes to thank the South African Museum and Field Museum of Natural History for allowing him to use their preparation facilities. Drs. Mike Raath and James Kitching, BPI in Johannesburg; Jacques van Heerden, formerly of

the National Museum in Bloemfontein; and Mike Cluver of the South African Museum kindly permitted one or both of us to study and borrow protosuchian material. The first author would like to acknowledge the aid of the Geology Foundation of the Department of Geological Sciences the University of Texas at Austin; he also thanks Dr. A.W. Crompton, Harvard University, who provided stereophotographs and the holotype of *Eopneumatosuchus colberti* for study, and Mr. James Clark for allowing him to look at *Protosuchus* material belonging to Berkeley that he is currently studying. Dr. Jaime Powell, Tucuman, kindly provided a cast of the recently re-prepared holotype of *Hemiprotosuchus lealii*. The shaded illustrations of BP-1-4746 were prepared by Ms. Claire Vanderslice.

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The postcranial skeletons of three fabrosaurids from the upper Elliot Formation "Red Beds" of the Stormberg Group in southern Africa are described. The material demonstrates details of fabrosaurid anatomy previously unknown, particularly a deep, deep prepubic process which is undoubtedly primitive for the Ornithischia. Besides the short prepubis, fabrosaurids are characterized by 1) a reduced manus; 2) an ilium having a lateral extension of the supra-acetabular margin and a deep nearly vertical broad shelf; and 3) an elongated hindlimb. Postcranial morphology excludes the fabrosaurids from the ancestry of the contemporaneous heterodontosaurids. Neither can the fabrosaurids be considered ancestral to the 'juvenile scelidosaurid' (BMNH R6704) as has been suggested. On the contrary, the 'scelidosaurid' is more primitive in structure than fabrosaurids. The assignment of *Nesotyrannus agilis* Marsh to the Fabrosauridae is not substantiated after morphological comparisons between the postcranial material of both. The taxonomic status of *Scutellostaurus lauderi* is regarded as uncertain. The fabrosaurids are more similar to the Morrison Formation camptosaurids, than to *Hypsilophodon*. Finally, it is argued that ornithopods were not a basal stock for the phylogenesis of non-ornithomorphs but represent an independent radiation comparable to the other ornithischian suborders. The fabrosaurids were an early development of the ornithopod radiation itself.

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INTRODUCTION

For many years it was thought that ornithischian dinosaurs appeared late in the Mesozoic since few unequivocal skeletal remains were known from earlier than the late Jurassic. This was in marked contrast to the saurischians which were relatively common in the later Triassic. The eventual recovery of early ornithischian material from late Triassic/early Jurassic deposits (Bonaparte 1976; Casamiquela 1967; Colbert 1981; Crompton and Charig 1976; Ginsburg 1964; Santa Luca, Crompton and Charig 1976; Simmons 1965; Thulborn 1970a, b, 1972, 1974) has disproven the notion of late evolving ornithischians. The next development in the assessment of early ornithischians was the recognition that they could not all be accommodated within the conservative ornithomorph family Hypsilophodontidae, as a direct result the families Heterodontosauridae (Kuhn 1968; Wever 1966) and

Fabrosauridae (Galton 1972) were erected to contain much of the new material. Finally, after a detailed analysis of some of the heterodontosaurid material, it became apparent that the morphological diversity displayed by the early ornithischians even went beyond the limits of the suborder Ornithopoda (Santa Luca, Crompton and Charig 1976; Santa Luca 1980).

At the present time most early ornithischian dinosaurs known are classed either as Fabrosauridae or as Heterodontosauridae (the status of the 'juvenile scelidosaurid', BMNH R6704, remains uncertain). The fabrosaurids represent an early lineage in the ornithopod radiation; they were small, around a metre in length, and probably obligate bipeds in locomotion. They were also fairly widely distributed geographically: they are known from the Stormberg localities in southern Africa, from the Kayenta formation of western North America, from the Jurassic of Portugal (Thulborn 1973) and