3.1.4 Description

3.1.4.1 The bones of the skull (Figs.10 and11)

Due to the loss of the whole skull border except some of the posterior border (which has been slightly distorted) reconstruction of the shape of the skull is subject to error. Also, the left lower jaw is attached firmly to the skull and a broken smooth-edged fragment of jugal lies loosely to the right of the right orbit.

Anterior to the midpoint of the frontal, the bone is severely damaged and no detail of sutures is evident. However, lateral line canals are easily recognized from anterior to the midpoint of the orbit.

The frontal:

Only the posterior and part of the lateral sutures of the frontal are visible. The lateral suture is slightly slanted towards the midline and the posterior suture is almost transverse and straight. This suture is indistinct but capable of being reconstructed. The frontal abuts the midline in a straight suture where visible.

The postfrontal:

The anterolateral edge of the postfrontal forms part of the posteromedial border of the orbit. The suture with the postorbital is straight and parallel to the midline and then slopes medially at an angle of $\pm 130^{\circ}$, where it sutures with the supratemporal; the anteromedial suture with the frontal slopes towards the midline; the posteromedial suture with the parietal slants posterolaterally. Thus the postfrontal is a roughly pentagonal bone pointed posteriorly between the parietal and supratemporal.

The postorbital:

The postorbital is also roughly pentagonal. The anterior edge of the bone forms the posterior border of the orbit. The anteromedial suture with the postfrontal is parallel to the midline; the posterolateral border slants towards the posterolateral corner of the skull. Anterolaterally the suture with the jugal (whose limits are unknown) is slightly slanted in a posterolateral direction while the posterolateral suture with the squamosal slants posteromedially. This results in the postorbital forming an obtuse point between the squamosal laterally and the supratemporal medially.

The parietal:

The medial suture of the parietal is a straight line. Halfway along this suture a circular parietal foramen is visible. The anterior suture with the frontal forms an almost straight transverse suture. This suture is badly

TABLE VI

STRATIGRAPHY

	SOUTH AFRICA		ZAMBIA	EAST AFRICA
TRIASSIC	UPPER	Cave Sandstone Red Beds Molteno		
	MIDDLE	Cynognathus	Red Marls? N'tawere Formation	Manda Formation
	LOWER	Lystrosaurus	?Escarpment Grits	?Kingori Sandstone

damaged. Anterolaterally, the parietal sutures with the postfrontal in a posterolaterally directed suture. Posterolaterally, the bone meets the supratemporal which forms a concave edge to the parietal. The posterior border of the parietal is laterally convex and medially slopes posteriorly so that together with the right side the parietal forms a sharp point in the midline.

The supratemporal:

This is a roughly pentagonal bone. The anterior suture with the postfrontal is slanted slightly posteriorly. The anterolateral suture with the postorbital is slanted posterolaterally so that the anterolateral corner of the supratemporal is almost a right-angle. The posterolateral border with the squamosal and most of the medial border with the parietal are more or less parallel to each other and slightly slanted posterolaterally. The posteromedial corner of the supratemporal abuts the postparietal in a posterolaterally directed curved suture. The posterior border of the supratemporal is parallel to the posterior border of the skull, suturing with the tabular posteromedially. The posterolateral corner of the supratemporal overlies part of the squamosal.

The squamosal:

Anteriorly the squamosal forms an acute angle between the postorbital medially and the remains of the jugal and quadratojugal laterally. The latter bones are missing, except for a narrow piece of jugal which lies disarticulated on the lateral side of the right orbit. The posterolateral corner of the squamosal was probably gently rounded. Posteromedially, the squamosal has a slightly slanted border with the supratemporal which appears to overlie the squamosal and a concave suture with the tabular (only the right tabular is preserved to some degree) at its posteromedial corner. The posterior dorsal edge of the squamosal turns at right-angles from the skull table to form an occipital flange which probably overlay most of the quadrate bone. The occipital flange of the squamosal is badly damaged, but it leaves an impression in the underlying matrix. This shows that the squamosal has a curved border above a large otic recess and expands ventrally to cover most of the quadrate.

The postparietal:

The anterior suture of the postparietal has a lateral concave and medial posteriorly slanted suture with the parietal. Medially the postparietal abuts the midline in a straight line; anterolaterally the postparietal forms a posterolaterally directed curved border with the supratemporal.

Posterolaterally the postparietal abuts the tabular in a short curved suture. The posterior dorsal edge of the postparietal forms the posterior border of the skull table. The postparietal then turns through 90° onto the occiput. The occipital flange of the postparietal when viewed dorsally is triangular in shape and when viewed laterally is a short round knob on the posterodorsal corner of the skull. In occipital view the postparietals form the roof over the large space above the foramen magnum that was probably occupied by the cartilaginous supraoccipital. Laterally the suture with the tabular is slightly dorsolaterally slanted. The postparietal is straight ventro-medially, then expands into a triangular flange. The lateral edge of this flange forms the dorsomedial corner of the post-temporal foramen.

The tabular:

Most of the right tabular is present. The anterior border is a transverse straight suture with the supratemporal. The lateral border is a postero-laterally slanted suture with the squamosal. The medial limit is a curved suture with the postparietal. The posterior dorsal border of the tabular forms part of the posterior limit of the skull. The tabular then turns through 90° to appear on the occipit. The ventral limit of the tabular is straight medially then laterally forms a ventromedially directed rounded pillar which sutures with the dorsolateral extension of the exoccipital and forms the posterolateral corner of the posttemporal foramen.

The quadrate:

The only part of the quadrate that is visible is the condyle. Seen posteriorly the condyle is shaped like a rounded triangle, the apex of which lies ventrally. A rounded articular boss lies most posteriorly with the bone expanded laterally and anteriorly from each side of this projection.

The exoccipital:

In lateral view, the exoccipital condyle is clearly seen with a rounded articular area. The foramen magnum is not visible in this view, only solid exoccipital is seen rising dorsally and anterolaterally from the condyle.

Seen posteriorly, each exoccipital forms an oval condyle. The condyles project approximately 3mm from the posterior end of the occipital flange of the postparietal. From the condyle a flange of exoccipital which borders the foramen magnum extends dorsally but is broken off a few millimetres above the condyle. Dorsolaterally to the condyle a broad flange of the exoccipital rises to meet the occipital flange of the postparietal. The exoccipital forms the wall of the occiput below the posttemporal foramen and lateral to it meets the occipital flange of the tabular.

Seen posteriorly the pterygoid meets the exoccipital below the otic recess. This suture is not visible. The pterygoid continues laterally in a smooth curve and then turns through 90° to form a vertical flange which continues ventrally internal to the squamosal. The bones are distorted in this region. The basioccipital is evidently not ossified.

3.1.4.2 The Sculpture

The superficial sculpture of the skull roof is of typical brachyopid pattern, similar to that found in capitosaurs and consists of pits in the centre of ossification of each bone, from which ridges and grooves radiate outwards, but show no areas of disproportionate growth, unlike in capitosaurs.

3.1.4.3 The Lateral Line System

The typical batrachosuchian 'lantern' pattern of the anterior lateral-line system is visible on the skull roof as a series of irregular pits which have slightly broader-based bordering ridges than those of normal sculpture. The distribution of the canals differs from the other two species but is closer to B. watsoni (Welles and Estes, 1969, p. 25).

The supraorbital canal: From the antero-lateral corners of the parietals the canals pass along the posterolateral sutures of the frontals and enter the prefrontals. Although the limits of the prefrontals and the nasals are damaged and not recognizable, the lateral line canals are visible. The supraorbital canals then turn medially and are lost to view.

The temporal canal: These canals run from the posterior border of the skull table where they form a curve, from the postero-medial borders of the post-parietals to the anterolateral limits of those bones. They then traverse the supratemporals from the posteromedial to the anterolateral corners displaying a sharp curve midway along their length. The temporal canals then enter the postfrontals medially along their posterolateral borders and continue straight on to the posterior borders of the orbits. From here they do not follow the pattern of the Batrachosuchus species as illustrated by Watson (1956), where the temporal canals continue laterally around the orbit as well. This is probably due to the fact that in B. concordi, where the relevant bones are present, the surface detail is damaged and obscure. In B. concordi, the temporal canals continue medially along the medial borders of the orbits to join the supraorbital canals halfway along the length of the orbits.

No other canals are discernible probably due to the fragmentation of the relevant bones and the sculpture pattern itself which makes it difficult to follow irregularities.

3.1.4.4 The Palate

Very little of morphological significance is preserved in the palate. Anteriorly, the choanae are visible as being transversely oval and relatively large. The stump of a large tusk is present lateral to each choana. The parasphenoid forms a flat plate which blends into the exoccipitals and pterygoids without a visible suture. Anteriorly, it sends out a cultriform process which is broad and flat.

The pterygoids extend outward from the parasphenoid until at their anterolateral extremity they end in a curved border, clearly part of the anteromedial limit of the subtemporal vacuity. Laterally, the pterygoids curve through 90^{o} to form vertical flanges. When viewed laterally, the pterygoid sweeps anterodorsally from the quadrate condyle posteriorly to a position directly ventral to the posterior border of the orbit. The ectopterygoid which sutures at this point with the pterygoid, continues anteriorly to a point beneath the anterior limit of the orbit. The pterygoid and ectopterygoid form a characteristic shape very similar to that illustrated by Watson (1956) for Batrachosuchus watsoni Haughton

The exoccipitals form rounded condyles which project outwards from the midline. Each condyle measures 5mm horizontally and 4mm vertically. The less distorted left condyle projects 3mm behind the dorsal edge of the skull table. The two condyles are 1.2mm apart and 12mm across. A flat parasphenoid separates the two condyles.

3.1.4.5 The Lower Jaw (Figs.12 and 13)

The jaw is bowed upward to match the concavity of the palate. The area between the symphysial region (the anterior part of which is missing in this specimen) and the adductor fossa is high and narrow and is inclined ventromedially. This area does not have a keeled ventral surface as in Blinasaurus henwoodi (Cosgriff 1969). In dorsal view the jaw widens through the region of the adductor fossa and the articular facet. A flat ventral surface underlies the anterior half of the adductor fossa. The ventral surface from the centre of the adductor fossa to the tip of the retroarticular process is keeled. The large adductor fossa is spear-shaped in dorsal view with a flat posterior margin and an acute anterior margin. The labial wall is very high and has a rounded upper margin. The lingual wall is low and its upper margin is concave downward. The articular facet is defined by pre- and post- condylar processes. Lingually, the articular facet forms a ledge which overhangs the surface of the jaw below it. The narrow retroarticular process is triangular in section. The posterior meckelian foramen is not preserved.

The left jaw ramus is firmly attached to the skull with the retro-articular process extending approximately 1cm behind the skull table. The right jaw ramus is free and seems to be almost undistorted, although the anterior part is missing.

The dentary: The dentary forms the tooth-bearing surface. Anteriorly there are two large teeth. Posteriorly and dorsally the dentary is capped by the coronoid. The dentary extend onto the labial wall of the adductor fossa as a slender and pointed process. Ventrally the dentary sutures with the remains of the second splenial anteriorly, then with the angular and posteriorly with the surangular.

The splenial: Only the posterior part of the second splenial is preserved. It lies ventral to the dentary and forms the antero-ventral border of the jaw ramus. Lingually, in the posterior portion, it is overlapped by the angular ventrally in a slanted suture and by the prearticular dorsally, which forms a tapered point extending onto the splenial. A very small part of the anterior border of the adductor fossa is bounded by the splenial.

The angular: The angular covers a large area on the labial surface, where it forms a suture with the splenial anteriorly, the dentary dorsally and the surangular posteriorly. The angular tapers to a long thin projection which borders most of the ventral surface of the ramus and curves to a fine point at the limit of the retroarticular process.

The dermal sculpture retained on the labial surface shows broad ridges and grooves of the typical labyrinthodont pattern that radiate out from the centre of the lower edge. There seems to be no angular-prearticular suture on the ventral surface of the jaw. The angular has a lingual process which abuts the prearticular in a straight longitudinal suture, midway along the lingual wall of the adductor fossa. According to Cosgriff (1969) a feature of the lower jaw that is diagnostic of the family as a whole is the position of the angular-prearticular suture which is on the ventral surface or very low on the lingual surface. Cosgriff (op. cit.) also states that a lingual process of the angular is lacking in *Batrachosuchus*; however, as this material is almost certainly of the Brachyopidae and probably a Batrachosuchian, this diagnostic feature no longer holds true.

The surangular: The surangular lies dorsal to the angular. Anteriorly, in the labial view, it forms a sharp point between the angular ventrally and the dentary dorsally. Posteriorly, the surangular is excluded from the glenoid fossa by the prearticular and articular. The surangular tapers to a ribbon of bone which extends to the limit of the retroarticular process.

The coronoid: Seen labially, the coronoid has a ventral suture with the surangular posterior to the dentary-surangular suture. In lingual view the coronoid sutures with the surangular and forms the antero-dorsal limit of the adductor fossa.

The prearticular: In labial view the prearticular has a small lateral exposure capping the precondyloid process, anterior to the glenoid fossa. In lingual view, anteriorly it forms the medial border of the adductor fossa, and ends in a slanted suture with the splenial. Ventrally, the prearticular meets the angular in a straight suture.

The articular: The articular forms the glenoid fossa and extends posteriorly to the limit of the retroarticular process, where it lies dorsal to the angular. The articular forms the whole glenoid fossa and terminates just anterior to this fossa. Seen from above, the glenoid fossa is roughly triangular, agreeing with the triangular quadrate.

Jaw mechanism: Because of the relatively large retroarticular process, a strong depressor mandibular muscle was probably present attached to the dorsal skull table where muscle ridges are discernible. The action of a powerful muscle here would open the jaw rapidly. The relatively large adductor fossa and the large area available for muscle attachment on the pterygoid and the underside of the skull roof indicates a strong adductor system consisting of the pterygoideus and adductor mandibular muscles to snap the jaw shut.

3.1.4.6 The Atlas (Fig.14 a-e)

The atlas is well preserved. It has a square centrum 10mm long in the ventral midline, 8mm from between the condylar articular facets to the notch of the axis articulation and 10mm across the anterior face. The exoccipital condyles fit perfectly into the anterior sockets which are spheroidal hollows separated by approximately 1mm. In Hadrokkosaurus bradyi (Welles and Estes 1969), the condylar facets are confluent ventrally, whereas in ?Batrachosuchus (Watson, 1956) from the Cynognathus zone, the condylar facets are separated by a "rather wide slightly hollowed and pitted surface". In B. concordi the condylar facets are also separated by a similar area.

The posteriorly directed neural arch rises from midway along the length of the centrum and consists of two pillars which fuse dorsally; the tip of the neural arch is broken off. On either side of the neural arch on the lateral surface of the centrum a deep indentation is present, probably for muscle attachment. The floor of the neural canal is wide and slightly hollowed along its length.

Ventrally the bone is more or less flat, unlike that of *Hadrokkosaurus* which has a ventral keel. The atlas of *?Batrachosuchus* also lacks a ventral keel.

In posterior view the atlas of *B. concordi* has a concave, vertically oriented, hemicylindrical facet. There is no notochordal pit, unlike that occurring in *Hadrokkosaurus*, but similar to that of *?Batrachosuchus*; *Batrachosuchoides lacer* (Shishkin 1966) includes an amphicoelous atlas which does not have a ventral keel.

3.1.4.7 The Axis (Fig.14 d-h)

Only the centrum is preserved with the floor of the neural canal clearly visible. The anterior articular facet is a vertical hemicylinder with a transverse concavity. This hemicylinder fits perfectly into the posterior concavity of the atlas and it is apparent that relatively large lateral angular movements of the atlas on the axis were possible. The ventral surface of the axis is more or less flat and slightly expanded posteriorly. The dorsal surface shows the concave hollowed floor of the neural canal on either side of which indentations occur in the centrum, which indicate the position of attachment of the neural arch. The axis of *B. concordi* does not resemble the presumed axis of *?Batrachosuchus* figured by Welles and Estes (1969, fig. 24 f-j) which has a different overall shape being less convex anteriorly and more or less triangular in lateral view. It also has deep excavations on the antero-dorsal face which evidently housed the axial pleurocentra. These features are not present in the atlas of *B. concordi*. The two vertebrae are similar in their posterior faces, where both are nearly circular. In *?Batrachosuchus* (Watson 1956) this face is pierced centrally by an opening for the notochord, while in *B. concordi* a circular depression approximately 1.5mm in diameter is present.

3.1.4.8 The Appendicular Skeleton (Fig.15)

All elements pertaining to the appendicular skeleton were diassociated but found in close proximity to the skull in the matrix. There can therefore be little doubt that they all pertain to the pectoral girdle and forelimbs. Dermal elements of the pectoral girdle are conventional and present no problem. The endochondral girdle and forelimb elements however differ markedly from all known labyrinthodont postcrania, including what little brachyopid material there is (Nillson 1939; Romer 1947; Watson 1956; Panchen 1959; Welles and Estes 1969; Howie 1970). In view of the above, only tentative identifications may be made at this stage.

<u>The pectoral girdle</u>: The bones figured as 'scapulo-coracoid' may possibly be cleithra as discussed later. Other than that there are many small sculptured fragments which do not give a clue as to their original part in the interclavicle/clavicle configuration, which are thin and smooth medially with fine sculpturing externally. Not much more can be said about these fragments.

There is a slight possibility that the 'scapulo-coracoid' elements are cleithra. These elements may be described as follows: they are gently curved elements which are expanded at both ends. There is no sculpture but the surface is finely pitted. On the inner surface of the curve there are no irregularities and the surface is smooth. On the outer surface of the curve, a ridge runs from end to end. The end nearest the midline as illustrated ends in a flat border, while the distal end is gently curved. The ridge on the outer surface starts at the anterior corner of the flat proximal head, runs straight along the anterior edge of the shaft until midway along the curve and then turns posteriorly to end midway along the curved distal end. Panchen (1959) described the cleithrum in typical labyrinthodonts as being a bony rod clasping the edge of the scapula in a deep groove. No such groove is found in the element described. Also these elements bear no similarity to any of the cleithra illustrated by Nilsson (1939). These elements could be part of the scapulo-coracoid except for the fact that there is no sign of any sort of glenoid fossa, or even an area of thickened bone. These bones may also be the humeri which possibility is discussed later.

To summarize, four postcranial elements which may or may not have been connected, may be either scapulo-coracoid elements, cleithra or humeri. The evidence one way or other is minimal.

<u>Forelimb elements</u>: Great difficulty is experienced in making identifications here due to the unavailability of comparative material. There is an added problem that this specimen may have been a young individual which increases the likelihood of the presence of extensive cartilage.

<u>The 'humerus'</u>: The bones already described as scapulae or cleithra may possibly be humeri. If they are humeri the rounded head probably lay proximal to the scapula. Extensive cartilage would of necessity be presumed. The anterior surface has a low wide ridge running the whole length of the

element from midway along the proximal head to the lateral edge of the distal head. The bone slopes down gently from the ridge so that the whole of the anterior surface is gently rounded, while the posterior surface is very concave. The proximal head lies at an angle of approximately 30° to the distal head; the proximal head is not at an angle to the shaft, rather the whole element is curved, smooth and featureless. These may not be humeri because there is no supinator process as described and figured by Welles and Estes (1969 fig. 25) for Batrachosuchus sp., nor is the shaft modified into the tetrahedral form common to the labyrinthodonts; and there are no deltoid or pectoral crests. Also the strong curve of the bone seems to suggest an alternative possibility, as the resultant of concurrent forces acting on a curved rather than a straight axis is greatly reduced. However these elements do show slight similarities to the humerus of Megalobatrachus maximus Schmalhausen (after Miner 1925) as illustrated by Nilsson (1939 fig. 8E, p.31)

The bone labelled ulna in the text figure may be a humerus. Two such elements were found, they may be described as follows: If they are humeri the more expanded head probably lay proximal to the scapula. Both proximal and distal ends were probably covered extensively by cartilage in life. The larger proximal surface of each element is gently rounded and relatively featureless except for an ovate articular area at the end of a wide ridge on the posterior edge of the ventral surface.

The slightly hollowed ovate articular area is turned obliquely at a 45° angle from the shaft. In primitive tetrapods this is typical in contrast to a strap-shaped proximal articulation of the humerus (Romer 1947). The proximal entepicondylar region tapers from the breadth of the head to the narrow posteriorly curved ectepicondylar border.

On the ventral surface there is one large ridge which extends the entire length of the element. At the distal end, this ridge divides into two confluent ridges from which the bone slopes at an acute angle to a dorsoventrally flattened plate. The ectepicondyle is a narrow ridge, the crest of which is smoothly rounded. The dorsal surface is smoothly rounded and featureless.

These elements may not be humeri because: there is no supinator process; the shaft is not modified into the tetrahedral form common to the labyrinthodonts; and there are no deltoid or pectoral crests. However, these elements do conform slightly to a general definition of the labyrinthodont humerus as given by Romer, 1947, as follows:

"Proximal and distal planes of the bony surfaces may be 'twisted' into a position at right angles to one another, or the two ends may be in the same plane. The proximal articulation, when well ossified exhibits an elongate spiral surface suited to articulate with the glenoid fossa. There is always a deltopectoral crest and frequently a projecting supinator process is present distally on the radial margin. This latter process may, however, be reduced or fused into a longitudinal ridge along the distal part of the margin of the bone. Beneath the ectepicondyle lies a rounded convex articular surface for the radius; medial (or posterior) to it a rounded terminal area articulates with the sigmoid notch in the ulna. The entepicondyle is always well-developed."

These elements bear a slight superficial resemblance to the humerus of Cacops aspihephorus Will (after Case 1911) as illustrated by Nilsson (1939, fig. 8c, p.31). However the strong curvature of that element seems to preclude this possibility.

The ulna: It is also possible that the bones labelled ulna and already described as the humeri may actually be the ulnae. If they are the ulnae, the question arises as to which other of the elements found could be the humeri. There are none, bar the 'scapula'; therefore the ulna bones have strong support for being humeri. However, as the possibility does exist that these bones are ulnae, the problem must be discussed further.

The ulnae may be described as follows: Proximally and distally the articular areas are ovate. Between the articular areas a large ridge runs anteriorly along the whole length of the bone. From the ridge the bone slopes at an acute angle to a wide flange distally, which narrows proximally. The whole bone is gently curved on the medial border, the lateral border has an outward bulge. Distally the posterior surface of the bone is smoothly rounded, almost straight and bowed-out distally. These bones may not be ulnae because: they are very large for ulnae and there is no evidence of an olecranon depression, although the olecranon process may have been cartilaginous.

There is a strong case for the radii being ulnae (they are figured as radii which is a possibility discussed later). They may be described as follows: The shaft is ovate proximally, becomes thin and rounded in the middle and becomes expanded distally in an anteroposterior plane. The medial border is gently curved and the lateral border is almost straight and slightly bowed-out proximally so that the proximal and distal ends of the bone are expanded towards the radius. The characteristic olecranon depression as well as the olecranon process are not preserved. If these bones are the ulnae, the radii are probably missing; some cylindrical smooth shattered fragments possibly belonging to the radii exist

An alternative description of the 'radii' bones as radii is as follows: The bones are columnar with proximal and distal ends expanded. Seen anteriorly, the gently incurved dorsal surface is rounded and the ventral surface is flattened. Both of the terminal surfaces are shallowly cupped for the rather extensive cartilages of the articular surfaces. There are no easily identified muscle origins or insertions. Thus, to summarize: of the fore-limbs, the bone figured as an ulna may be that or the humerus; the bone figured as the radius may be that or the ulna.

Ribs: Of the remaining broken remnants of the skeleton, a few can be recognized as ribs; most show portions of narrow shafts and are clearly doubleheaded. These presumably were from the trunk or neck region.

3.1.5 Discussion

It is quite clear that this material belongs to the family Brachyopidae because of the following characteristics:

1. It has a short broad skull and large anteriorly placed orbits.
2. There are no otic notches and no tabular horns.
3. There are very large palatal tusks.
4. It has a strongly sloping occiput and a deep cheek region.
5. It has a highly vaulted palate.
6. There is a pronounced squamosal-quadratojugal trough on the occiput lateral to the pterygoid; the latter is expanded posteriorly.

In general shape, B. concordi most resembles Batrachosuchus watsoni Haughton (1925) except for size; the skull of B. watsoni is approximately 15.7cms in length and that of B. concordi is approximately 4.8cms long.

The differences between B. watsoni, B. browni and B. concordi are:

1. The occipital condyles do not project as far posteriorly in B. concordi as in B. watsoni, although the occipital condyles seem to be proportionately the same size. In B. browni the occiput extends further posteriorly than in B. watsoni, but this may be due to a transverse crack in B. browni.
2. The lateral line system in B. watsoni is very much more pronounced than in B. browni. In B. concordi, the lateral line canals are barely visible, but where found follow the characteristic paths of those of the batrachosuchians.
3. An interfrontal is absent in B. watsoni, but present in B. browni. In B. concordi the presence of an interfrontal is indeterminate.

4. The shapes of the individual bones of the skull roof are essentially the same in B. concordi as in the two batrachosuchian species where the sutures can be positively identified.
5. The shape of the posterior skull table is slightly convex, which agrees with B. watsoni, but not B. browni. (Further preparation has revealed a parabolic crack in B. browni which passes through the pineal foramen; the crack is filled with matrix, this distorts the posterior curvature of the skull).
6. The skull of B. concordi is much narrower than in both B. browni and B. watsoni, but it is closer in breadth to B. browni (B:L). This character of B. concordi may be a juvenile feature.
7. The interorbital breadth is very much narrower than in the other two larger forms. This is a primitive feature which could also be a juvenile character (A:L).
8. The preorbital length of B. concordi is slightly shorter than the other two forms (O:L).
9. The relative orbit length of B. concordi is approximately the same as in the other two species (U:L).
10. The postorbital length is midway between B. browni and B. watsoni (D:L).
11. The interpterygoid vacuity is almost the same relative length as B. browni and B. watsoni (Q:R).
12. The interpterygoid vacuity is narrower than in both of the other forms, being closest to B. browni (Y:L).
13. An index Welles and Estes (1969) did not use, i.e. the distance of the parietal foramen in front of the back of skull table: midline length of skull (T:L) shows that in B. concordi it is greater than in both B. browni and B. watsoni (T:L = 23); (T:L in B. concordi = 37), i.e. the parietal foramen in B. concordi is more anteriorly placed on the skull than either of the other two forms.
14. A lingual process of the angular is present in B. concordi which Cosgriff (1969) states is absent in Batrachosuchus.
15. The parasphenoid in B. concordi reaches the posterior edge of the skull between the exoccipitals as in B. watsoni. In B. browni, the parasphenoid does not reach the end of the skull.

In the reconstruction certain changes are made to the skull. These are illustrated in Table VII as differences in the measurements obtained by measuring directly off the skull and measuring from the reconstruction.

These differences are:

(a) the height of the postparietals above the condyles has been raised in the reconstruction as the postparietals definitely display a dorso-ventral depression which probably did not exist in life;

(b) the breadth across the quadrates is greater, as the bones lateral to the squamosal are missing and have been inserted in the reconstruction from illustrations of Batrachosuchus watsoni, as illustrated by Watson (1959) and Batrachosuchus browni as redescribed here;

(c) the length of the skull is consistent with that of the reconstruction as some of the preorbital bones are present in the skull although badly damaged and the postorbital region has been reduced in the reconstruction. These two reasons, i.e. the presence of preorbital bones in the skull and the shortening of the postorbital region (which is discussed later) keep the skull length constant;

(d) the interorbital distance is shorter in the reconstruction as the borders of the left orbit are extremely distorted where not actually missing;

(e) the distance from the tip of the snout to the level of the anterior edge of the orbit is greater in the reconstruction as the maxilla and premaxi [illegible]a have been inserted in the reconstruction as being similar to those of B. browni and B. watsoni;

(f) midline postorbital length has been shortened in the reconstruction because in this region the bones are not closely sutured, but have considerable gaps between them. These gaps are removed in the reconstruction;

(g) the distance from the mid-line of the orbit to the lateral edge of the same side is increased in the reconstruction because only the right side of the skull gives any indication of this area and even here only a small disarticulated part of the jugal lies next to the orbit though somewhat displaced In the reconstruction, a larger jugal is added lateral to the orbit to cover the underlying pterygoid completely (in dorsal aspect) which seems to be more or less in its correct position;

(h) the breadth of the snout one-fifth of the skull length from the tip of the snout is narrower in the reconstruction than would appear to be the case from the photograph, as the left lower jaw is firmly attached dorsally on the lateral part of the skull;

(i) the distance from the level of the posterior limit of the orbit to the parietal foramen is less in the reconstruction because as mentioned above, the gaps between the bones in the skull are not present in the reconstruction.

Welles and Cosgriff (1965) adopted a method of analysis for capitosaurs whereby a series of arbitrary measurements is made on the skulls and indices are then derived from these measurements. Comparison of these indices lead to significant phylogenetic and taxonomic conclusions. The validity of the conclusions is dependent upon the accuracy of the measurements, the number of characters that are susceptible to numerical analysis and the number of specimens available.

Welles and Estes (1969) developed this method by assuming that the sum of the differences between indices for any two species is a useful indication of the relationship between these species, which can then be compared with the sum of the differences between indices for any other two species. They acknowledge the various shortcomings of this method of analysis of which the most serious is that even though large numbers of species are included, there is a strong likelihood that in any group with a long geologic time span, those forms at a similar stage of evolution will be closer together numerically than later forms in a phylogenetic sequence. If there is a large number of specimens from each species, this objection can be reduced by measuring differences from trend lines if such exist. This was useful in the analysis of capitosaurs (Welles and Cosgriff, 1965) but it is of less value in dealing with the small number of known brachyopids. However, nine of the indices used by Welles and Estes (1969) do show trends and these are probably indicative of the relative evolutionary level of the various genera.

Other objections are that non-numerical characters are excluded from this analysis and must be considered separately, but adequate knowledge of ontogenetic changes within a species is not available nor is it known just how much or how little these changes affect the validity of the indices.

Nevertheless, as Welles and Estes (1969) point out, this index method of analysis does have the advantage of presenting in tabular form a series of summaries that are not otherwise readily comprehensible. This methodology can only be improved with accurate data, and it is important that accompanying every description of a specimen accurate indices are included. By the collection of such data the probability of the validity of the results is increased so that a revision every few years including new data should add to the clarity of our understanding of the group.

The reconstruction of the specimen is an essential ingredient in this flow of data. Where much of the skull is shattered, missing or severely distorted, measurements taken directly off the skull are misleading and bear no relationship to indices taken from undistorted skulls, thus the onus falls on the palaeontologist to reconstruct with the utmost accuracy (i.e. as far as the specimen allows) a skull which takes into account the limitations of the material.

In conclusion, index methodology is important with regard to many aspects of palaeontology, and it should be regarded as standard practice to include in descriptions accurate data which can be used in the future to correlate the mass of information which has been and is being collected.

Indices for *B. concordi* :

B : L	118	D : L	57	Q : R	30
A : L	28	P : A	75	Y : L	46
O : L	17	T : A	107	Z : Y	52
U : L	25	H : B	19		

Sums of differences	Using 6 indices	Using 11 indices
Batrachosuchus concordi / *Hadrokkosaurus bradyi*	82	224
B. concordi / *B. watsoni*	35	110
B. concordi / *B. browni*	37	121
B. concordi / *B. laticeps*	59	168
B. concordi / *Blinasaurus henwoodi*	44	111
B. concordi / *Bothriceps australis*	43	122
B. concordi / *Brachyops allos*	52	142

Using 11 indices *B. concordi* seems to be closely related to *Blinasaurus henwoodi*. The T : A index which is not included for the computation of the 6-index figure is the reason for this low figure. *Blinasaurus henwoodi* and *Batrachosuchus concordi* both have orbits relatively very close together, compared with other brachyopids, but as far as *B. concordi* is concerned, this character seems to be a juvenile feature. Thus it may be possible to add another shortcoming of the methodology, i.e. a young individual may show similar proportions to an unrelated adult form at a different evolutionary level. However, other than the above disparity assuming that the smaller totals of index differences are real measures of relationship, the conclusion reached that B. concordi is a batrachosuchian seems to be correct.

Thus it is possible that B. concordi is of the genus Batrachosuchus but a new species. It could possibly be a small member of either B. browni or B. watsoni, but for two characteristics which may not be completely explained by ontogenetic growth, i.e. the close proximity of the orbits and the very small projection of the occiput. There is a possibility that the orbits move laterally during growth, but the sculpture in the interorbital bones is pitted, rather than having ridges and grooves. According to Bystrow (1935) and Welles and Cosgriff (1965) longitudinal grooves are probably regions of intense growth and where growth is slow, transverse ridges are able to develop so that such bones consist mostly of pits. Thus it seems unlikely that the interorbital region was in a state of intense growth that would be needed to separate the orbits to a position comparable to either B. browni or B. watsoni. If it is a juvenile form of one or other of the batrachosuchians it would more likely be a small B. watsoni as the parasphenoid of B. concordi as in B. watsoni, extends to the edge of the skull, whereas in B. browni the parasphenoid does not reach the edge.

3.1.6 Summary

(1) Batrachosuchus concordi is erected for the material No. F 3728 from Locality 15 of the N'tawere Formation of the Upper Luangwa Valley, Zambia.

(2) According to the evolutionary scheme of the brachyopids as discussed by Welles and Estes (1969), B. concordi confers a Lower-Middle Triassic age for Locality 15.

TABLE VII

Batrachosuchus concordi - showing differences in measurements between reconstruction and fossil

	Directly from skull (average mean of 5 measurements in cms	From reconstruction in cms
Height of postparietals above parasphenoid H	0.9	1
Breadth of skull across quadrates B	5.2	5.7
Length of skull L	4.8	4.8
Interorbital distance taken at mid-length of orbit A	1.6	1.3
Distance from tip of snout to level of anterior edge of orbit O	0.5	0.8
Distance from level of posterior limit of orbit to level of centre limit of skull D	3.1	2.8
Distance from mid-length of orbit to lateral edge of same side I	0.2	0.6
Breadth of snout 1/5th of skull length from tip S	3.7	3.5
Distance from level of posterior limit of orbit to parietal foramen taken at centre of skull P	1.3	1.0
Distance of parietal foramen in front of end skull table T	1.6	1.8

TABLE VIII

MEASUREMENTS OF THE SKULLS OF THE GENUS BATRACHOSUCHUS

	B. browni cms.	B. watsoni* cms.	B. concordi cms.
Interorbital breadth, A	9	5	1.3
Breadth of skull roof across quadratojugals, B	24	16.5	5.7
Midline postorbital length, D	10	7.0	2.8
Midline distance between nostrils and orbits, F	3.0	1	0.4
Height of parasphenoid, H	4,5	3.5	1
Internarial breadth, J		1.1	
Length of skull roof, L	20	11.5	4.8
Midline preorbital length, O	4.8	2.4	0.8
Distance behind orbits of parietal foramen, P	5	3.3	1.0
Length of body of pterygoid, Q	4.9	3.4	1.5
Breadth across pterygoids at concavity, R	18	11.2	5
Distance of parietal foramen in in front of end skull table, T		3	1.8
Breadth of snout 1/5th of skull length from tip, S	16	9.2	4
Midline orbital length, U		2.5	1.3
Length of interpterygoid, Y	10	5.7	2.4
Breadth of interpterygoid, Z	6.6	3.3	1.4
Distance between choanae, G	4.9	3	1.3
Distance exoccipital projects behind skull deck	5	2	0.3

* From Welles and Estes (1969) p.24

3.2 Batrachosuchus browni Broom 1903

Type: Skull only. S.A.M., Cat. No. 5868

Locality: Aliwal North, Cape Province

Horizon: Cynognathus zone

3.2.1 Diagnosis

Large brachyopid with broadly parabolic skull outline; orbits far forward, postorbital part of skull long; extremely narrow internarial area; interfrontal present; lateral line grooves well defined, but relatively much narrower and possibly more U-shaped in section than in B. watsoni; well developed vomerine foramen in centre of vomer; parasphenoid does not reach posterior limit of skull; three lateral line canals present on postfrontal; evidence of paired tusks on vomer, palatine rectopterygoid.

3.2.2. Material and Method of Preparation

The material consists of a well preserved skull whose antero-lateral borders are missing. The skull does not seem to be very distorted. Additional preparation was undertaken on the skull by Dr. J. Kitching by means of a vibro-tool and needles.

3.2.3 Differential Diagnosis

Compared to Batrachosuchus watsoni: according to Welles and Estes (1969) "B. watsoni is very close to B. browni, but has more extreme (advanced) values for 6 of 9 characters. The main differences, relative to skull length are: very much broader skull than B. browni, narrower internarial area (thought to be more primitive), greater interorbital breadth, longer preorbital region, shorter orbits and longer postorbital deck, longer body of pterygoid and broader interpterygoid vacuity". These differences according to Welles and Estes (1969) are at least of specific degree and might even justify erection of a new genus. However, they consider B. watsoni a more advanced species with a much broader skull than B. browni.

Welles and Estes (1969) in comparing B. browni with Brachyops state: "Relative to skull length the skull is slightly narrower; the nares are much closer together; the orbits are almost equally far apart, extremely far forward and exactly the same length; the postorbital part of the skull table is very long; and the interpterygoid vacuity is very short. In relation to interorbital breadth, the parietal foramen is closer to the orbits and farther from the back of the deck. The vomer is longer relative to its breadth, and the length of the pterygoid compared with the breadth across the pterygoids is slightly greater. The interpterygoid vacuity is narrower relative to its own length. Batrachosuchus is thus very closely related to Brachyops".

Welles and Estes (1969) continue: "Compared with Bothriceps, Batrachosuchus browni shows many of the same differences as in Brachyops but to a slightly greater degree. Relative to the skull length, the skull is much broader; the nares are closer together; the orbits are much farther apart and extremely far forward; the orbits are about the same length, but the postorbital deck is very long; the interpterygoid vacuity is very short. In relation to interorbital breadth, the parietal foramen is the same distance behind the orbits and not nearly so far from the end of the skull table. In palatal view, the vomerine plate is considerably broader relative to its length; the pterygoid is about the same length relative to the breadth across the pterygoid; and the interpterygoid vacuity is much broader relative to its length".

Welles and Estes (1969) compare B. browni with Blinasaurus as follows: "Relative to skull length, the skull of Batrachosuchus browni is much broader, the internarial width is greater; the orbits are extremely far apart; the preorbital snout is much shorter; the orbits are smaller; the postorbital deck is much longer, and the interpterygoid vacuity is much shorter. In palatal view the vomerine plate is much broader relative to its length, and relative to breadth across the pterygoids, the body of the pterygoid is much shorter. The interpterygoid vacuity is broader relative to its own length".

Welles and Cosgriff (1967) compare Batrachosuchus with Hadrokkosaurus as follows: "The skull of Batrachosuchus is narrower, the nares very close together; the orbits are also closer together. The preorbital skull table is shorter; a much longer postorbital skull table. Relative to interorbital width, the parietal foramen is much further from the orbits, but about the same distance from the end of the postparietal. In palatal view, the vomerine plate is much longer and narrower; and the pterygoid body is very slightly longer relative to the breadth across the pterygoids. In relation to skull length, the interpterygoid vacuity is shorter. Relative to its own length, the interpterygoid vacuity is narrower. In Hadrokkosaurus the vertical flange of the pterygoid extends much farther posteriorly than in B. browni".

Cosgriff (1973) compares Batrachosuchus watsoni with Notobrachyops as follows: " The skull is much broader, the orbits are much farther apart; the preorbital skull table is much shorter. In Notobrachyops, each bone of the skull is elevated in the ossification centres and depressed at the sutural edges. Also, in Notobrachyops, the posterior edge of the skull roof is strongly convex and evenly curved between the otic embayments".

3.2.4 Description (figs.16 and 17)

3.2.4.1 The bones of the skull

The antero-lateral limits of the skull are missing; no premaxillary or maxillary sutures are discernible and only the posterior half of the right narial border is preserved as an impression. Unless otherwise stated the left side of the skull is described, because the bones on the right hand side have suffered some displacement and slight damage.

The nasals: The posterior part of the right nasal is preserved. The mid-line suture is sinuous; posteriorly the nasal sutures with the inter-frontal in an anterolaterally slanted suture. Laterally part of the suture with the prefrontal is visible as a posteromedially slanted suture, so that at the posterolateral corner, the nasal forms a sharp point. The posterior suture with the prefrontal is curved.

The interfrontal: The interfrontal is roughly diamond-shaped bone with its anterior extremity lying between the two nasals and its posterior end between the frontals. It is widest at the naso-frontal suture.

The prefrontal: The prefrontal forms part of the anterior border of the orbit but the exact limits are not visible. The posterior border with the postfrontal is curved laterally towards the orbit. Part of the antero-lateral suture with the nasal is visible; this slants medially. Postero-laterally the prefrontal sutures with the frontal in a laterally slanted suture so that the lateral border of the prefrontal has an obtuse angle approximately halfway down its length.

The frontal: The frontal is a fairly large bone; anteromedially the posterior half of the interfrontal is wedged between the two frontals. Lateral to the interfrontal suture, the frontal curves round suturing with the nasal anteriorly and the prefrontal anterolaterally. The lateral limit of the frontal is a more or less straight suture with the postfrontal. The posterior suture with the parietal differs on each side; on the right side it is straight, while on the left it has a small projection into the parietal.

The postfrontal: The postfrontal forms the posteromedial border of the orbit. Anteriorly the suture with the prefrontal curves anteromedially. The anterolateral suture with the frontal is more or less straight. The anterolateral corner of the postfrontal forms a sharp point between the prefrontal and the frontal. The posterolateral suture with the parietal is slanted posterolaterally so that the lateral suture of the postfrontal has an obtuse angle along its length. Laterally the suture with the postorbital is almost transverse anteriorly and parallel to the midline posteriorly, so that the lateral border of the postfrontal forms a rough right angle along its length. The posterior border of the postfrontal is straight and almost transverse.

The postorbital: The postorbital is a roughly pentagonal bone. The anterior median part forms the posterior border of the orbit. On either side of the orbital border formed by the postorbital the anterior sutures meet with the jugal laterally and the prefrontal medially and are almost transverse and straight, sloping slightly posteriorly. The medial suture with the prefrontal forms a rough right angle; posteromedially, the postorbital sutures with the supratemporal in a posterolaterally slanted suture. The anterolateral suture with the jugal is almost parallel to the midline. Posterolaterally, the suture with the squamosal is anteromedially directed so that the apex of the rough pentagon is solely projected into the squamosal and not between the squamosal-supratemporal suture.

The jugal: The lateral limits of the jugal are not preserved. Anteriorly the jugal enters the orbit in an almost straight posterolaterally directed suture. Anterolaterally the suture with the postorbital is also slanted in a posterolateral direction and also enters the orbit. Thus the posterolateral border of the orbit is formed by the jugal. Posterolaterally, the jugal meets the postorbital in an almost straight suture parallel to the midline. Posteriorly, the jugal sutures with the squamosal in a curved posterolaterally directed suture.

The parietal: The parietal is longer and wider than the frontal. The anterior suture with the frontal is curved on the left and almost straight and transverse on the right. A circular parietal foramen lies just