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A NEW BRACHYOPID, *BATRACHOSUCHUS CONCORDI* SP. NOV. FROM THE UPPER LUANGWA VALLEY, ZAMBIA WITH A REDESCRIPTION OF *BATRACHOSUCHUS BROWNI* BROOM, 1903

by

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ABSTRACT

Two brachyopid skulls from southern Africa are described: one from the N'tawere Formation, Zambia is assigned to *Batrachosuchus concordi* sp. nov. and the other, *B. browni* Broom from the *Cynognathus* zone of South Africa is used as comparative material after further preparation had been effected on it. Both are assessed in relation to published descriptions of *B. watsoni* and it is concluded that *B. concordi* is closest to *B. watsoni*. The possibility that *B. watsoni* and *B. browni* belong to the same species is discounted for the present as there are four distinct differences in their skull morphology. Some poorly preserved and enigmatic bones from immediately behind the occiput of *B. concordi* are interpreted as limb and girdle elements. Associated with these bones are an axis and an atlas. All three species are at about the same level of organisation and that helps confirm that the *Cynognathus* zone of South Africa and the N'tawere Formation of Zambia are of approximately the same age and span the Lower-Middle Triassic boundary.

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INTRODUCTION

The brachyopid labyrinthodonts existed from the Upper Permian to the Upper Triassic. Some reached six feet in length and all are characterized by large orbits, a ∩-shaped palate, a long retroarticular process and a more or less parabolic skull outline.

Watson (1919, 1956), Cosgriff (1969) and Welles and Estes (1969) are among those who have reviewed the contents and taxonomic history of the family. Based on work by previous authors, a composite diagnosis of the family Brachyopidae may be given as follows: skull short and broad; B : L index 110 to 150; no zones of relative intensive growth; occipital condyles project well behind posterior edge of skull roof; basicranial joints absent; pterygoid bones joined by suture to parasphenoid bones; squamosal and quadratojugal with strong occipital flanges forming a vertical, transversely concave trough lateral to the pterygoid; pterygoid forming a large vertical plate laterally which is posteriorly elongated beyond squamosal-quadratojugal trough, making a steeply arched flat-roofed palate.

Workers have at various times removed genera and families from the Brachyopidae. Panchen (1959) removed the plagiosaurs from the family. Cosgriff (1969) removed the Dvinosauridae, forming a separate family, which together with the Brachyopidae constitute the Superfamily Brachyopoidea. Welles and Estes (1969) removed *Dvinosaurus primus* Amalitzki 1921, because of its primitive structure as indicated by the lack of development of the pterygoid-parasphenoid suture. They also removed the following species: *Tungussogyrinus bergi* Efremov 1939, from the Korwuntchan (upper Angara) series near Tungus, Siberia; *Boreosaurus thorslundi* Nilsson 1943, from the Early Triassic of Spitsbergen; *Pelorocephalus mendozensis* Cabrera 1944, from Potrerillos Village, Mendoza Province, Argentina, in the Upper Cacheuta beds of Early or Middle Triassic age; *Tupilakosaurus heilmani* Nielsen 1954, from the Early Triassic of Greenland; *Enosuchus breviceps* Efremov (in Konjukova) 1955, from the Russian Zone II (Late Permian) of the Isheevo site in the Tatar A.S.S.R.; *Eobrachyops townendae* Watson 1956, from the Upper Permian Clear Fork beds of Texas; *Indobrachyops panchetensis* Huene and Sahni 1958, from the Upper Panchet rocks (Early Triassic) of India; *Plagiorophus paraboliceps* Konjukova (1955) from the Early Triassic Zone V of Chkalov province, U.S.S.R.

The species retained in the Brachyopidae are:

(i) *Brachyops laticeps* Owen 1855. Only one specimen (B.M.N.H. No. R4414) was found from the Mangali beds in Nagpur, Central India (possibly equivalent to the *Lystrosaurus* zone). A composite definition of *Brachyops laticeps* Owen 1855 is: small brachyopid with parabolic skull; snout tapered to point; large orbits anterior to mid-length of skull; antero-posterior axis of orbits directed parallel to skull border; very large choanae; cultriform process of parasphenoid overlain by vomer; no denticles present on cultriform process; lateral line grooves relatively narrow; sculpture pattern linear.

(ii) *Bothriceps australis* Huxley 1859. Only one specimen comprising a skull and attached incomplete lower jaw (B.M.N.H. No. 23110) has been found from an unknown locality in Australia. The midline length of the skull is approximately 8 cm. A composite definition of *Bothriceps australis* is: small brachyopid with narrow skull; skull roof roughly triangular in dorsal view; large orbits set close together, relatively far back on skull roof; preorbital length of skull roof is 33 % of skull length; broad subtemporal fossa, indented on medial margin by a projection of the Pterygoid bone.

(iii) *Blinasaurus wilkinsoni* (Stephens) Cosgriff 1969
= *Platyceps wilkinsoni* Stephens 1887
Proc. Linn. Soc. N.S.W. 2, 1175–1195
= *Bothriceps wilkinsoni* (Stephens) Lydekker 1890
Q. Jl. geol. Soc. Lond., **46**, 289–294
= *Platyceps wilkinsoni* (Watson 1956)
Bull. Br. Mus. nat. Hist. (Geol.), **2**, 317–391.

A partial skeleton (N.S.W.G.S. No. F12872) consisting of the skull roof, a number of branchial bars, the dermal shoulder girdle and a series of ribs and vertebral elements was found at the Railway Ballast Quarry near Gosford, New South Wales, in the uppermost part of the Gosford Formation, Narrabeen Group (Middle Triassic).

A composite definition of *Blinasaurus wilkinsoni* is: very small brachyopid with narrow parabolic skull; orbits close together; parietal foramen very close to orbits; in dorsal view skull nearly circular.

(iv) *Blinasaurus henwoodi*, Cosgriff 1969. A fairly complete skull (W.A.M. No. 62.1.42) found in the Erskine Range on Blina Station, West Kimberley District, Western Australia, from the Upper Blina Shale, *? Otoceraton* Division of the Scythian Stage. The skull is approximately 11,2 cm in length.

A composite definition of *Blinasaurus henwoodi* is. small brachyopid with narrow parabolic skull; orbits close together; parietal bone separated from postorbital bone by postfrontal-supratemporal suture; frontal forms part of medial margin of orbit.

(v) *Bothriceps major* Woodward 1909. This specimen, from the Late Permian Upper Coal Measures, Airly, New South Wales, consists of a skull and associated partial skeleton, which was divided after its discovery, part remaining at the Mining Museum of the New South Wales Geological Survey as No. F12697, and part sent to the British Museum (B.M.N.H. No. R3728). The portion at the Mining Museum contains the dorsal impression of the skull roof (length of skull approximately 15,3 cm), the part described by Woodward (1909).

Watson (1919 and 1956) commented on the portion in the British Museum, redescribed and re-illustrated B.M.N.H. No. R3728 and placed the species in a new genus, *Trucheosaurus*.

Cosgriff (1969) retains the name *Trucheosaurus major* for this specimen. A composite definition of this species is: large brachyopid with skull roughly triangular in dorsal view; preorbital length of skull 34 % of skull length; orbits relatively smaller and more widely spaced than in *Bothriceps australis;* orbit length 20 % of total skull length; tabulars longer than in *B. australis.*

(vi) *Batrachosuchus browni* Broom 1903. (Redescribed below)

(vii) *Batrachosuchus watsoni* Haughton 1925. The specimen (B.M.N.H. No. 3589) is a complete skull (skull length approximately 12 cm) found in the *Cynognathus* zone (Lower-Middle Triassic?) of the Burgersdorp district, C.P., South Africa (Watson, 1956). It was first described by Watson (1919) as *Batrachosuchus* sp.

A composite definition of *Batrachosuchus watsoni* is: large brachyopid with broadly parabolic skull outline; orbits far forward, postorbital part of skull long; interpterygoid vacuity short; narrow internarial area; lateral line grooves well defined and broad.

(viii) *Batrachosuchus lacer* (Shishkin 1966)
(Batrachosuchoides lacer, Shishkin 1966)

This species is based on the anterior part of a skull, along with much fragmentary referred material from the Early Triassic Federov horizon, Baskunchakskaia Series, Viatki Basin, European U.S.S.R. This is a small brachyopid, about two-thirds the size of *Batrachosuchus watsoni.* Welles and Estes (1969) comment on this species: "In the generic diagnosis Shishkin (1966) lists a number of features, with nine derived from the type and three more based on referred material. The present state of our knowledge of brachyopid skull details is so poor that it is not possible to diagnose a genus or even a species on the basis of the characters listed." Welles and Estes draw no conclusions from the available and scanty data, but as yet find no reason to exclude the Viatki brachyopid from the genus *Batrachosuchus*.

(ix) *Hadrokkosaurus bradyi* (Welles) 1947. This species was originally described as *Taphrognathus bradyi* (Welles 1947) but the generic name was found to be preoccupied and was changed to *Hadrokkosaurus* Welles (1957). The type, U.C.M.P., No. 36199, is a nearly complete right ramus of a lower jaw found in the Holbrook Member of the Moenkopi Formation some 10 km west of Holbrook, Arizona (probably Lower-Middle Triassic). The hypodigm contains skull material; length of skull approximately 23,4 cm.

A composite definition of *Hadrokkosaurus bradyi* is: extremely large brachyopid with smoothly parabolic skull outline; nares far apart; broad interpterygoid vacuities; quadrate ramus of pterygoid a vertical plate projecting far behind squamosal; lower jaw smooth-surfaced; large lateral mandibular fenestra.

(x) *Boreosaurus thorslundi* Nilsson 1943. The material included in this taxon by Nilsson consists entirely of lower jaw fragments from the Sticky Keep Formation of Spitsbergen (Lower Triassic). Welles and Estes (1969) exclude this genus from the Brachyopidae because of the very short retro-articular process.

Cosgriff (1969), however, includes this species in the Brachyopidae believing that the retroarticular process of the holotype was broken off close to its base and was probably elongate as in other brachyopids. A composite definition of *Boreosaurus thorslundi* is: jaw very slender; posterior meckelian foramen and angular-prearticular suture located low on lingual surface of lower jaw; adductor fossa long and narrow; jaw ramus bowed strongly upward in lingual view; labial wall of adductor fossa very high.

(xi) *Brachyops allos* Howie 1972. The specimen (Queensland Museum No. F.6572) consists of a more or less complete skull (skull length approximately 11,1 cm) found in Locality 0,6 Duckworth Creek, South Central Queensland. The horizon is the Lower Upper Rewan Formation of the Mimosa Group (Lower Triassic).

A composite definition of *Brachyops allos* is: brachyopid with more or less triangular shaped skull; small orbits anterior to mid-length of skull with the antero-posterior axis directed parallel to skull border; exoccipital condyles very near to level of quadrate condyles; sloping portion of occiput greatly reduced; cultriform process of parasphenoid clasped laterally by posteriorly directed processes of vomer; denticles present on posteromedial portion of cultriform process; long tripartite anterior palatal foramen.

(xii) *Notobrachyops picketti* Cosgriff 1973. This specimen (New South Wales Geological Survey No. F.8258) consists of an external impression of most of a skull roof (length of skull approximately 3,1 cm) and part of the right lower jaw ramus. It was found at the Huntsville Brick Company quarry, Mortdale, New South Wales. The horizon is the Ashfield Shale of Liverpool sub-group, Wiannamatta Group of the Sydney Basin (?Upper Triassic).

A composite definition of *Notobrachyops picketti* is: very small brachyopid with narrow skull and round snout; antorbital portion of skull roof approximately one-third of skull length; orbits close together; each element of skull roof elevated in central region and depressed around sutural edges; posterior edge of skull roof strongly convex.

(xiii) *Austrobrachyops jenseni* Colbert and Cosgriff,

TABLE I

World Distribution of Brachyopidae

	U.S.A.	SPITZBERGEN AND U.S.S.R.	INDIA	AFRICA	AUSTRALIA	ANTARCTICA
UPPER TRIASSIC					*Notobrachyops picketti*	
MIDDLE TRIASSIC	*Hadrokkosaurus bradyi*			*Batrachosuchus concordi* *Batrachosuchus watsoni**	*Blinasaurus wilkinsoni*	
LOWER TRIASSIC		*Batrachosuchus lacer* *Boreosaurus thorslundi*	*Brachyops laticeps*	*Batrachosuchus browni**	*Blinasaurus henwoodi* *Brachyops allos*	*Austrobrachyops jenseni*
UPPER PERMIAN					*Bothriceps australis* *Trucheosaurus major*	

* *Cynognathus* zone of South Africa which may well be Scythian (Cruickshank, 1967)

1974. This species was based on a left pterygoid bone more or less intact (American Museum of Natural History No. 9346) from Coalsack Bluff and a referred fragment of lower jaw (A.M.N.H. No. 9301) from Graphite Peak in the Transantarctic Mountains. These two localities are approximately 140 km apart. The horizon is the lower part of the Fremouw Formation (Lower Triassic).

A composite definition of *Austrobrachyops jenseni* is: brachyopid in which the pterygoid bone possesses a distinct angle in the middle of its course; ventrolateral corner of stapedial fossa incised by groove for internal carotid artery; labial wall of adductor fossa of lower jaw considerably higher than lingual wall; retroarticular process three times longer than articular facet; labial surface bears sculpture of elongate pits; oral and mandibular grooves well marked.

SYSTEMATIC PALAEONTOLOGY

In the following paragraphs *Batrachosuchus concordi* sp. nov. from the Upper Luangwa Valley, Zambia is described. Also, *Batrachosuchus browni* Haughton is redescribed, as the type specimen has been further prepared revealing more detail and some new characters.

Batrachosuchus concordi sp. nov.

Holotype. BPI Cat. No. F3728. Imperfect skull, lower jaws and some postcranial material

Locality. N'tawere Formation, Upper Luangwa Valley, Zambia. Locality 15 (Drysdall and Kitching, 1961)

Horizon. ? Lower Middle Triassic

Derivation. From a fancied similarity to the Concord supersonic airliner as seen in lateral view.

Diagnosis

Small *Batrachosuchus* with skull narrower than *B. browni* and much narrower than *B. watsoni*; interorbital breadth very much narrower than both; shorter preorbital length than both; orbit slightly smaller than *B. browni*; postorbital length greater than *B. browni*, but shorter than *B. watsoni*; interpterygoid vacuity shorter than *B. browni* and much shorter than *B. watsoni*, interpterygoid vacuity narrower than in both; distance of parietal foramen in front end of skull table greater than *B. browni* (T : L = 23) and *B. watsoni* (T : L = 23), (*B. concordi* T : L = 37); lateral line canals weakly defined; parasphenoid extends to basal limit of skull; exoccipital does not reach as far posteriorly as in either *B. watsoni* or *B. browni*; a lingual process of the angular is present.

Stratigraphy (see table 3)

This specimen was collected from the Upper Horizon of the N'tawere Formation by Drysdall and Kitching in 1961. The fossiliferous beds of their Locality 15 consist of dark red, soft mudstones with characteristic feldspathic grit bands, containing angular vein-quartz fragments. The N'tawere Formation contains two fossiliferous zones, the Lower with *Diademodon,* and an Upper (Red Marl) horizon which includes Locality 15. Towards the base of the beds, amphibians and molluscs are present. The molluscs have been identified as *Unio karrooensis* by Drysdall and Kitching (1963, p. 22). From the same locality, two cynodonts were also collected, the smaller perhaps belonging to the genus *Trirachodon,* and the larger a *Scalendon*-like form resembling material described by Crompton (1955) from the Manda Beds of Tanganyika.

The author has previously described two large capitosaurs from Locality 15 (Chernin and Cruickshank, 1970; Chernin, 1974; Chernin and Cosgriff, 1975) which were assigned to the species *Parotosaurus megarhinus.* This species is very similar to *P. pronus* (Howie, 1970) but distinct from it and perhaps somewhat stratigraphically older. *P. pronus* was collected from Mkongoleko, Ruhuhu Valley, Tanzania in the Manda Formation of East Africa (Middle Triassic) by Parrington, 1933.

Welles and Estes (1969) state that comparison of certain indices obtained by measuring the brachyopids shows trends which are probably indicative of the relative evolutionary level of the various genera. Of the 10 values obtained for the indices of *B. concordi,* one is more advanced than that of the *Cynognathus* zone batrachosuchians as given by Welles and Estes (the author has included her own values obtained by measurement of *B. browni*; Welles and Estes 1969 indices appear in parenthesis):

U : L = 23 — *B. watsoni*
23 — *B. browni* (24)
25 — *B. concordi*

Two values lie between the other species:

Q : R = 31 — *B. watsoni*
27 — *B. browni* (26)
30 — *B. concordi*

D : L = 58 — *B. watsoni*
50 — *B. browni* (55)
57 — *B. concordi*

Five values are more primitive than the other two species:

B : L = 149 — *B. watsoni*
120 — *B. browni* (133)
118 — *B. concordi*

A : L = 46 — *B. watsoni*
45 — *B. browni* (43)
28 — *B. concordi*

O : L = 25 — *B. watsoni*
24 — *B. browni* (21)
17 — *B. concordi*

Y : L = 53 — *B. watsoni*
50 — *B. browni* (49)
46 — *B. concordi*

Z : Y = 56 — *B. watsoni*
66 — *B. browni* (55)
52 — *B. concordi*

Finally two values are so much more advanced as to be out of the range of the Brachyopidae as considered by Welles and Estes:

P : A = 69 — *B. watsoni*
55 — *B. browni* (55)
80 — *B. concordi*
T : A = 49 — *B. watsoni*
55 — *B. browni* (53)
107 — *B. concordi*

The latter two values are the result of the interorbital breadth being so small in *B. concordi*. This could be a juvenile feature (no growth series of the Brachyopidae is available for study). However, taking the other indices as evolutionary guides, it seems that *B. concordi* is more or less on the same level as the *Cynognathus* zone forms. Welles and Estes (1969) place the batrachosuchians between Early and Middle Triassic. This agrees with the earlier conclusion that the N'tawere Formation is probably of Early Middle Triassic age (Chernin and Cosgriff, 1975) (see table 3).

Material and Method of Preparation

The material consists of a weathered and badly shattered skull, slightly dorsoventrally compressed with the anterolateral borders missing. Both lower jaw rami are present, the left one being firmly attached to the skull; the right one has been freed. The anterior parts are missing. A little of the postcranial skeleton is preserved, including parts of the pectoral girdle and forelimbs.

The skull is badly cracked, making the sutures difficult to discern. The material was prepared by Dr C. E. Gow who used a weak acetic acid solution.

TABLE 2
Comparison of the Indices of the Genus *Batrachosuchus*

* Indices	*B. watsoni**	*B. browni**	*B. browni****	*B. concordi*	From direct skull measurements of *B. concordi*
B:L	149	133	120	118	107
A:L	41,6	43	45	28	33
O:L	25	21	24	17	9
U:L	23	24	23	25	—
D:L	58	55	50	57	64
P:A	69	55	55	75	80**
T:A	49	53	50	107**	100**
Q:R	31	26	27	30	29
Y:L	53	49	50	46	52
Z:Y	56	55	66	52	50

* From Welles and Estes (1969).
** Out of range of Brachyopidae as stated by Welles and Estes (1969).
*** As measured in the new reconstruction of *B. browni*.

TABLE 3
Stratigraphy

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

Modified after Drysdall and Kitching (1963)

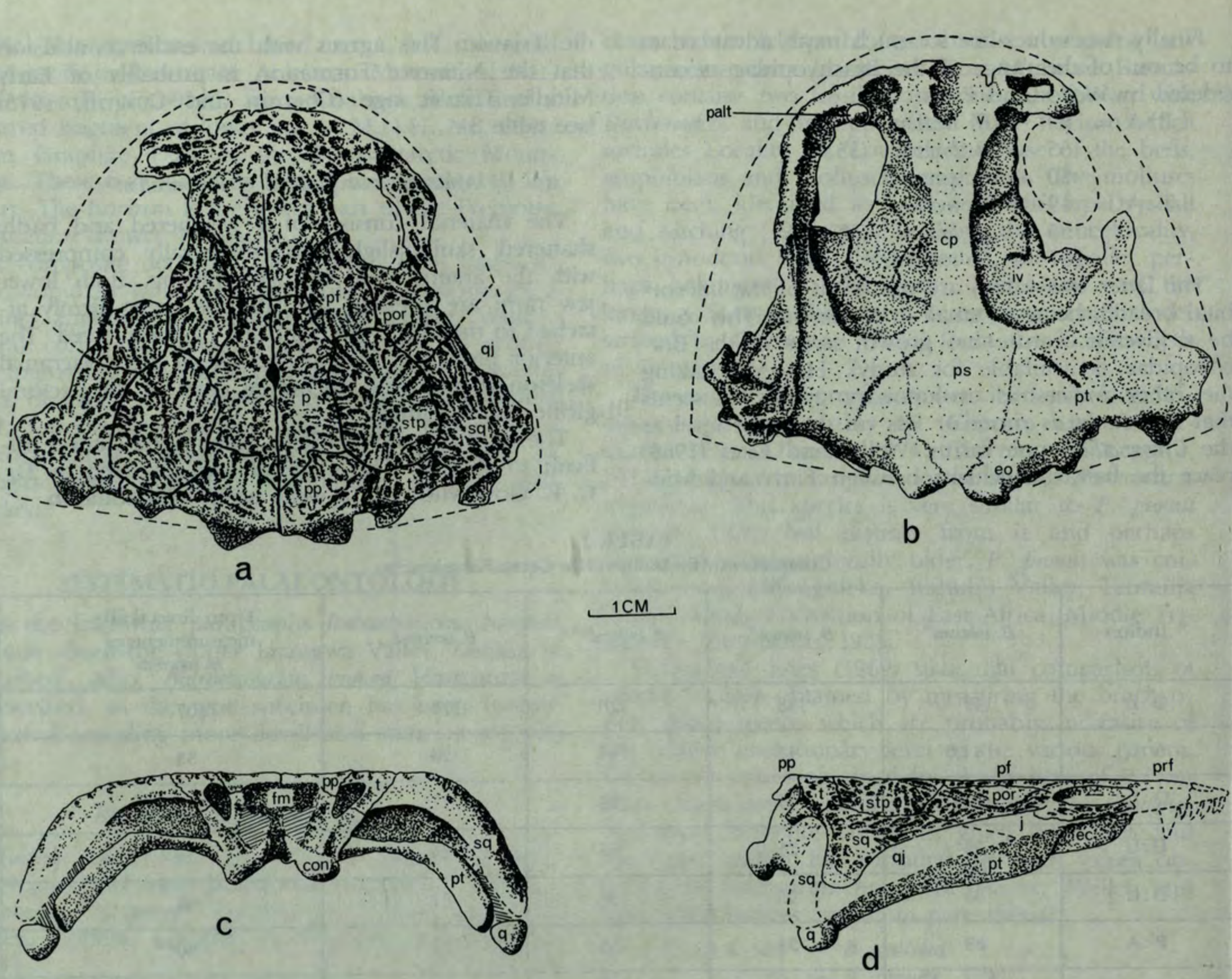

Figure 1. The skull of *Batrachosuchus concordi*
(a) dorsal view
(b) palatal view
(c) occipital view
(d) lateral view

Description

The bones of the skull (figs. 1 and 7)

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.

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 somewhat indistinct posterior suture is almost transverse and straight.

Postfrontal. The postfrontal is a roughly pentagonal bone pointed posteriorly between the parietal and supratemporal and anterolaterally the 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, where it sutures with the supratemporal; the anteromedial suture with the frontal slopes towards the midline.

Postorbital. The postorbital is also roughly pentagonal. The anterior edge of the bone forms the posterior border of the orbit. 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.

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 is almost straight. This suture is badly damaged. 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 the parietals form a sharp point in the midline.

Supratemporal. This is a roughly pentagonal bone. 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 abuts the postparietal in a posterolaterally-directed curved suture. The posterior border meets the tabular posteromedially. The posterolateral corner of the bone overlies part of the squamosal.

Squamosal. Anteriorly the squamosal forms an acute angle between the postorbital medially and the jugal and presumed position of the 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 was probably gently rounded. Posteromedially, the bone has a slightly slanted border with the supratemporal and a concave suture with the tabular. The posterior dorsal edge turns at right angles from the skull table to form an occipital flange which probably overlay most of the quadrate bone. The occipital flange is badly damaged, but it leaves an impression in the underlying matrix. This shows that the bone has a curved border above a large otic recess and expands ventrally to cover most of the quadrate.

Postparietal. The anterior suture of the postparietal has a lateral concave and medial posteriorly slanted suture with the parietal. Anterolaterally it forms a posterolaterally directed curved border with the supratemporal. Posterolaterally the postparietal abuts the tabular in a short curved suture. The bone turns through 90 ° on to 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 bones form the roof over the large space above the foramen magnum that was probably occupied by the cartilaginous supraoccipital. The lateral edge of the postparietal forms the dorsomedial corner of the posttemporal foramen.

Tabular. Most of the right tabular is present. The anterior border is a transverse straight suture with the supratemporal. The tabular has both an occipital and dorsal component. The ventral limit 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.

Quadrate. The only part of the quadrate that is visible is the condyle. Seen posteriorly this 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.

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, which project approximately 3 mm 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 rises to meet the occipital flange of the postparietal.

On the occiput the pterygoid meets the exoccipital below the otic recess. The 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.

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.

The Lateral Line System

The characteristic 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 that of the other two species but is closer to *B. watsoni* as illustrated by Welles and Estes (1969, p. 25).

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.

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 postparietals 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.

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° 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 5 mm horizontally and 4 mm vertically. The less distorted left condyle projects 3 mm behind the dorsal edge of the skull table. The two condyles are 1,2 mm apart and 12 mm across. A flat parasphenoid separates the two condyles.

Lower Jaw (figs. 2 a–c)

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. Lingually, the articular facet

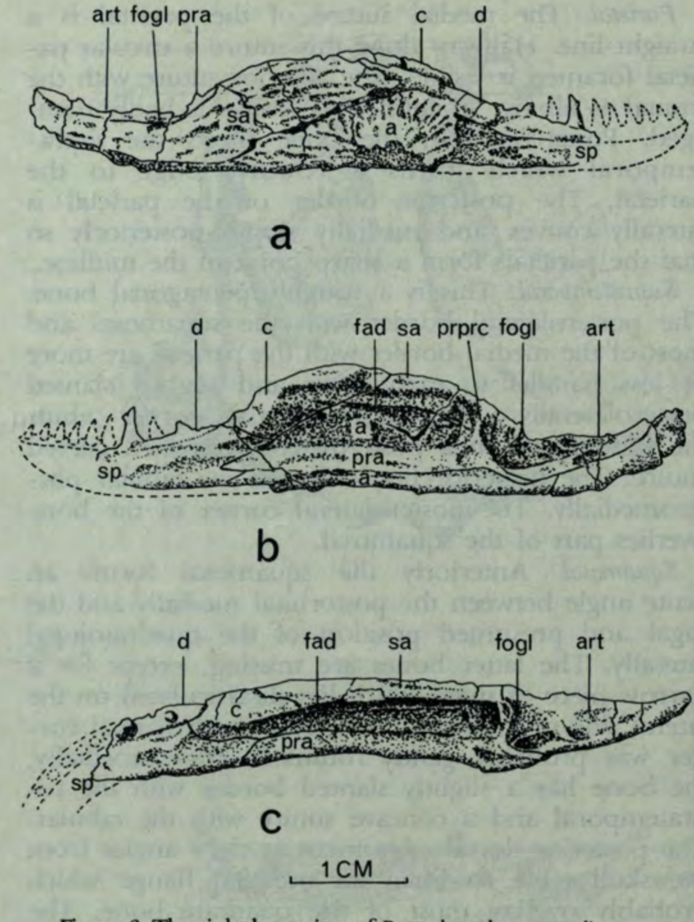

Figure 2. The right lower jaw of *Batrachosuchus concordi*
(a) labial view
(b) lingual view
(c) dorsal view

of the glenoid 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 retroarticular process extending approximately 1 cm behind the skull table. The right jaw ramus is free and seems to be almost undistorted, although the anterior part is missing.

Dentary

Anteriorly there are two large teeth. Posteriorly and dorsally the dentary is capped by the coronoid. The dentary extends on to the labial wall of the adductor fossa as a slender and pointed process.

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.

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.

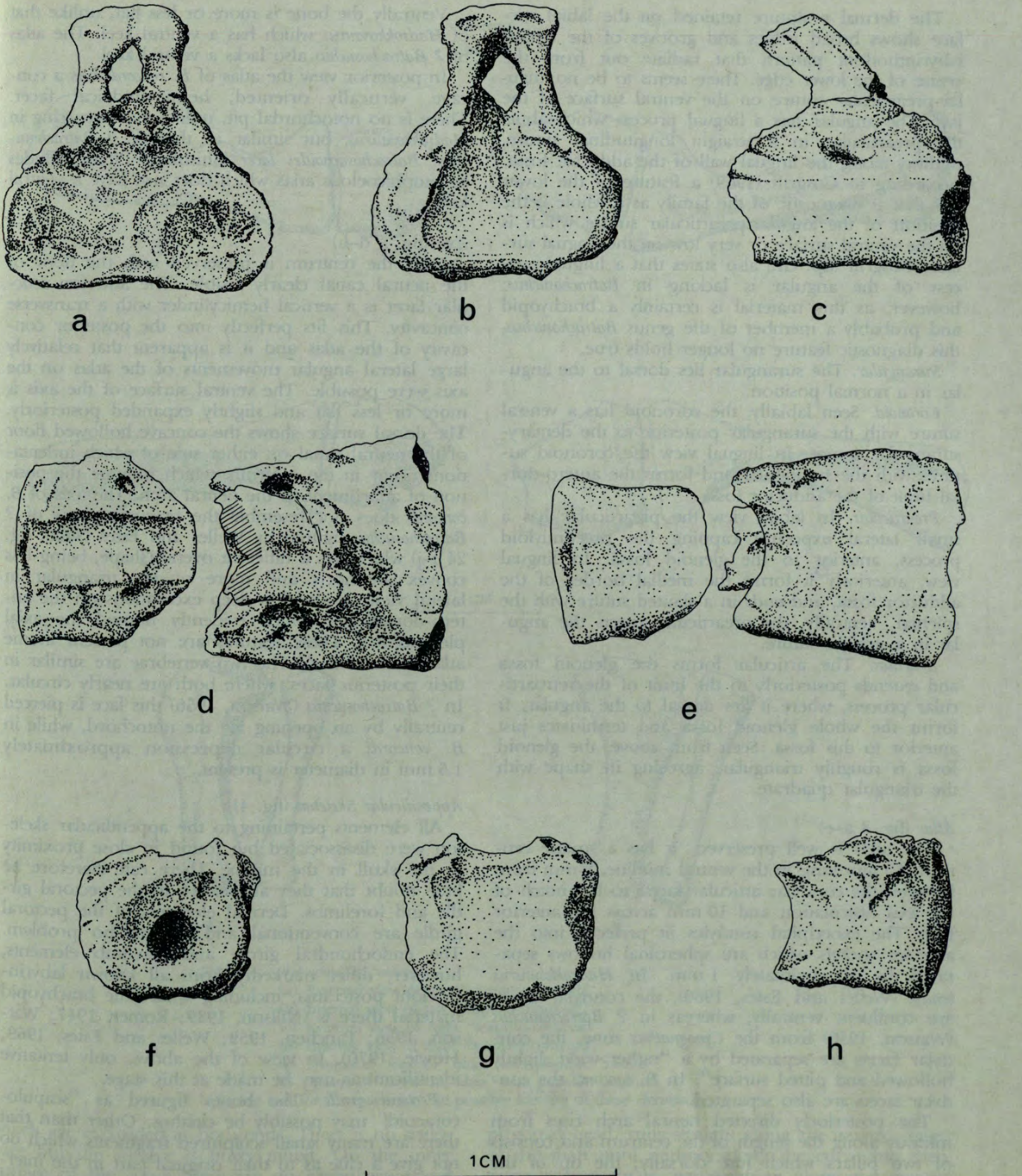

Figure 8. *Batrachosuchus concordi*

(a) Anterior view of atlas
(b) Posterior view of atlas
(c) Lateral view of atlas
(d) Dorsal view of atlas and axis
(e) Ventral view of atlas and axis
(f) Posterior view of axis
(g) Anterior view of axis
(h) Lateral view of axis

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 certainly a brachyopid and probably a member of the genus *Batrachosuchus*, this diagnostic feature no longer holds true.

Surangular. The surangular lies dorsal to the angular in a normal position.

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.

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.

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

Atlas (fig. 3 a–e)

The atlas is well preserved. It has a square centrum 10 mm long in the ventral midline, 8 mm from between the condylar articular facets to the notch of the axis articulation and 10 mm across the anterior face. The exoccipital condyles fit perfectly into the anterior sockets which are spheroidal hollows separated by approximately 1 mm. 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.

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.

Axis (fig. 3 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 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 1,5 mm in diameter is present.

Appendicular Skeleton (fig. 4)

All elements pertaining to the appendicular skeleton were disassociated 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.

Pectoral girdle. The bones figured as "scapulo-coracoid" may possibly be cleithra. 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.

The scapulo-coracoid/cleithra elements may be described as follows: they are gently curved elements

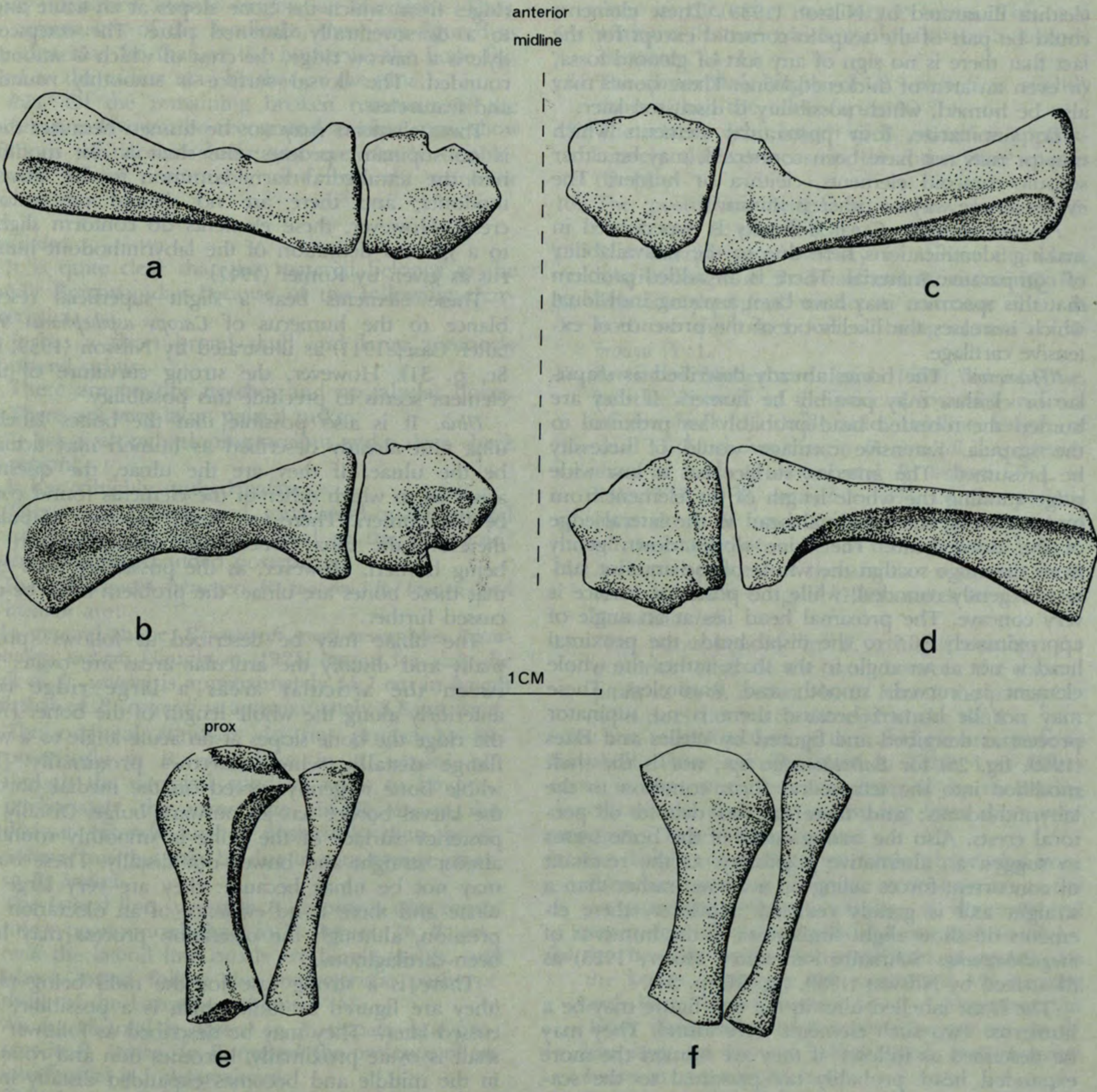

Figure 4. *Batrachosuchus concordi*
(a) External view of left "scapulo-coracoid"
(b) Internal view of left "scapulo-coracoid';"
(c) External view of right "scapulo-coracoid"
(d) Internal view of right "scapulo-coracoid"
(e) "Anterior" view of "ulna" with possible "radius"
(f) "Posterior" view of "ulna" with possible "radius"
N.B. See text for discussion on the possible identity of these 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 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.

Forelimb elements. 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.

"Humerus". 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* 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).

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.

Ulna. It is also possible that the bones labelled ulna and already described as 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 forelimbs, 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 double-headed. These presumably were from the trunk or neck region.

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.

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

In general shape, *B. concordi* most resembles *Batrachosuchus watsoni* Haughton (1925) except for size; the skull of *B. watsoni* is approximately 15,7 cm in length and that of *B. concordi* is approximately 3,8 cm long.

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 other 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, which 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 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 4 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 premaxilla 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 (fig. 6).

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

TABLE 4
Batrachosuchus concordi — **showing differences in measurements between reconstruction and fossil**

	Directly from skull (mean of 5 measurements) in cm	From reconstruction in cm
Height of postparietals above parasphenoid, H	0,9	1,0
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

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 is reached that the new material is indeed a species of the genus *Batrachosuchus*.

Batrachosuchus concordi 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 and it is known that the occipital region acquires a greater posterior projection during development in anurans. 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 *Batrachosuchus* 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.

TABLE 5
Measurements of the skulls of the Genus ***Batrachosuchus***

	B. browni cm	*B. watsoni** cm	*B. concordi* cm
Interorbital breadth, A	9,0	5,0	1,3
Breadth of skull roof across quadratojugals, B	24,0	16,5	5,7
Midline postorbital length, D	10,0	7,0	2,8
Midline distance between nostrils and orbits, F	3,0	1,0	0,4
Height of parasphenoid, H	4,5	3,5	1,0
Internarial breadth, J		1,1	
Length of skull roof, L	20,0	11,5	4,8
Midline preorbital length, O	4,8	2,4	0,8
Distance behind orbits of parietal foramen, P	5,0	3,3	1,0
Length of body of pterygoid, Q	4,9	3,4	1,5
Breadth across pterygoids at concavity, R	18,0	11,2	5,0
Distance of parietal foramen in front of end skull table, T		3,0	1,8
Breadth of snout 1/5th of skull length from tip, S	16,0	9,2	4,0
Midline orbital length, U		2,5	1,3
Length of interpterygoid, Y	10,0	5,7	2,4
Breadth of interpterygoid, Z	6,6	3,3	1,4
Distance between choanae, G	4,9	3,0	1,3
Distance exoccipital projects behind skull deck	5,0	2,0	0,3

* From Welles and Estes (1969, p. 24)

Batrachosuchus browni Broom 1903
Type: Skull only. S.A.M. Cat. No. 5868
Locality: Aliwal North, Cape Province
Horizon: Cynognathus zone

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 post-frontal; evidence of paired tusks on vomer, palatine ectopterygoid.

The differences between *B. watsoni* and *B. browni* 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*.

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. W. Kitching by means of a vibro-tool and needles.

Description (figs. 5 and 8)

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.

Nasals. The posterior part of the right nasal is preserved. The mid-line suture is sinuous; posteriorly the nasal sutures with the interfrontal in an antero-laterally slanted suture. Laterally part of the suture with the prefrontal is visible as a posteromedially

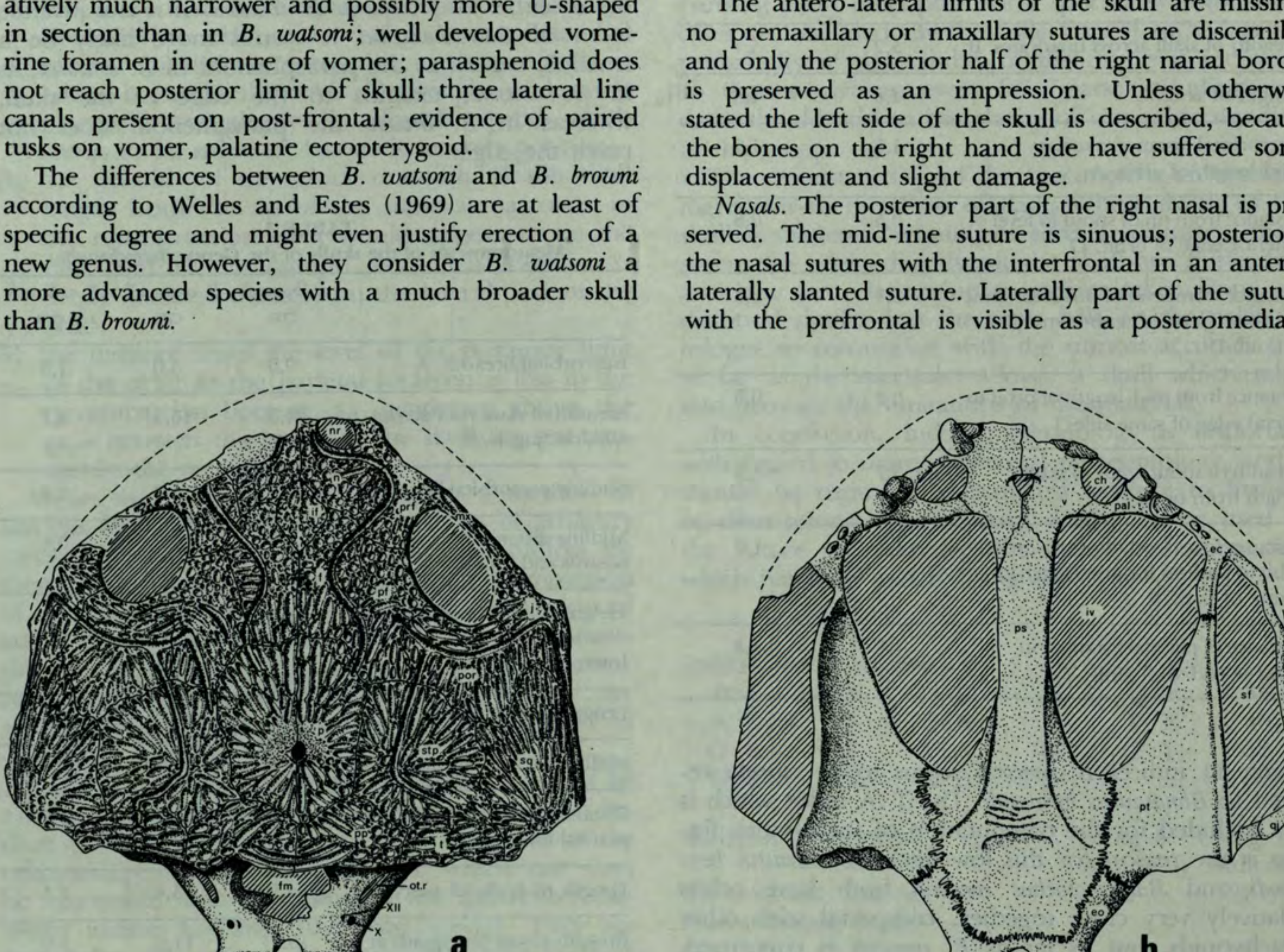

Figure 5. The skull of *Batrachosuchus browni*
(a) dorsal view
(b) palatal view
(c) occipital view
(d) lateral view

slanted suture, so that at the posterolateral corner, the nasal forms a sharp point. The posterior suture with the prefrontal is curved.

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.

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 anteromedial suture with the nasal is visible.

Frontal. The frontal is a fairly large bone; anteromedially the posterior half of the interfrontal is wedged between the two frontals. The lateral limit of the bone is a more or less straight suture with the postfrontal.

Postfrontal. The postfrontal forms the posteromedial border of the orbit. 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 forms a rough right angle along its length. The posterior border is straight and almost transverse.

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 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.

Jugal. The lateral limits are not preserved. The postero-lateral border of the orbit is formed by the jugal. Posteriorly, the jugal sutures with the squamosal in a curved suture.

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 posterior to the mid-length of the bone. Posterolaterally, the suture with the supratemporal is more or less parallel to the midline on the right side of the skull and posteromedially slanted on the left side of the skull. The posterior border of the parietal is also different on either side of the midline. On the right side it is almost straight and transverse, while on the left medially it projects into the postparietal and lateral to this rounded projection it is almost straight and transverse, so that its posterior limit forms a rough point.

Supratemporal. Laterally, the supratemporal sutures meet with the squamosal in a sinuous suture almost parallel to the midline. The posterior limit medially is a curved suture with the postparietal, while laterally the suture with the tabular is firstly straight and then turns suddenly posteriorly so that the supratemporal forms a sharp point between the tabular and postparietal.

Squamosal. The lateral limits of the bone are not preserved. It forms most of the dorsolateral border of the skull, then turns through 90 ° to form a large occipital flange whose lateral edge forms the dorsolateral wall of the otic recess. In occipital view its ventral edge meets the occipital flange of the quadratojugal (which is not seen on the skull roof) in a straight, almost transverse, suture.

Postparietal. Anteriorly the postparietal sutures laterally with the supratemporal. On the right side of the skull, the postparietal seems to have pushed the parietal anteriorly so that it appears larger than the left postparietal. The lateral suture with the tabular is almost straight and parallel to the midline. The postparietal forms the posterior border of the skull table in the midline and then turns through 90 ° to form an occipital flange which ventrally sutures with the vertical flange of the exoccipital. Seen posteriorly, the ventromedial limits of the postparietals form the roof of a transversely elongate opening that probably housed a cartilaginous supraoccipital. The ventrolateral edge of the bone in occipital view forms the medial border of the posttemporal fenestra. Dorsolaterally, it meets the occipital flange of the tabular in a straight, dorsolaterally slanted suture.

Tabular. The tabular forms a slightly curved suture anteriorly with the supratemporal. Medially it meets the postparietal in a straight suture parallel to the midline. The lateral suture with the squamosal is also straight and parallel to the midline on the right. The tabular forms part of the posterior border of the skull table, then turns through 90 ° to form an occipital flange which joins with the dorsolateral flange of the exoccipital, in an interdigitated angled suture. Ventromedially, the tabular forms the lateral and dorsal borders of the posttemporal fenestra. Ventrolaterally the bone forms the dorsolateral corner of the otic recess. Seen posteriorly, it meets the squamosal in a straight dorsolaterally slanted suture.

Exoccipital. Seen posteriorly, each exoccipital forms a rounded condyle from which two thick processes rise dorsally and one thinner process laterally. The exoccipital condyles project 5 cm beyond the edge of the skull table. Anterolateral to the condyle is a large foramen for the exit of the Xth nerve and just posterolateral to this is a second smaller foramen for the exit of the X11th nerve. The vertical postparietal process has two medial extensions, the larger dorsal one, the *processus lamellosus,* evidently underlay a cartilaginous supraoccipital. The ventral process, the *processus basalis,* which is a small, sharp projection, overlies the space presumably occupied by the cartilaginous basioccipital. Thus the true foramen magnum is smaller and narrower than the dorsal opening with its long axis transverse to the midline. Dorsolaterally the bone meets the tabular in a suture which has an acute angle halfway along its length. The dorsolateral limit of the bone forms the ventromedial border of the otic recess. The lateral process meets the pterygoid in a dorsolaterally directed suture.

In palatal view each exoccipital forms a rounded condyle posteriorly and extends anterolaterally to suture with the pterygoid in an interdigitating posterolaterally directed suture. Its medial suture with the body of the parasphenoid is curved and interdigitated.

Sculpture

The surface sculpture is exceptionally well preserved, consisting of round or rectangular pits in the centres of ossification from which ridges and grooves radiate outwards. Along some of the longer grooves cross struts have formed. A striking feature of the sculpture occurs on the postparietals and parietals where the sculpture pattern forms two triangles with their bases on the midline and the apices extending laterally towards the quadrates. The anterior angle of each triangle extends into the parietal and fades before reaching the parietal foramen. This pattern is different from that of *Hydrokkosaurus bradyi* (Welles and Estes, 1969), where the sculpture pattern is also triangular and extends to the midline of the frontals. However, both patterns include the centres of the postparietals.

Lateral Line System

The lateral line system conforms to Watson's (1956) illustration of *B. browni* except for one detail; within the left postfrontal three separate canals are visible and not two. The new canal is almost parallel to the midline, extending from just behind the anterior one-third of the postfrontal and fading just anterior to the posterior suture of that bone. It lies between the temporal and the supraorbital canal.

Supraorbital canal. This canal forms an hour-glass pattern in the centre of the skull. Posteriorly each groove enters the anterolateral corners of the parietals. From this point the groove curves laterally passing through the postfrontal. It then swings medially into the frontal. Halfway along the length of the frontal the groove changes direction and curves laterally again to exit from the frontal at its anterolateral corner. The groove then continues laterally into the prefrontal, where anteriorly it changes direction again, curving medially to leave the prefrontal at its anterior suture. The groove continues into the nasal following the curve of the nare. It fades at the medial border of the nare.

Temporal canal. The temporal canal issues from the postorbital and circles the orbit anteriorly giving off a posteriorly directed branch which crosses the postorbital at its posteromedial corner, and passes into the supratemporal and enters the tabular midway along the suture. The temporal canal which passes into the postfrontal sends off another branch which swings posteriorly to enter the anterolateral corner of the supratemporal where it stops. Also from the postorbital a lateral branch extends onto the jugal where it turns posteriorly and extends along the lateral part of the squamosal.

Palate

Unless otherwise stated the left side of the skull is described. The antero-lateral borders of the palate are not preserved, but a striking feature is the presence of a large foramen situated in the centre of the vomer on the midline. The position of this foramen seems to correspond to the cartilaginous area in *Hadrokkosaurus bradyi* (Welles and Estes, 1969). In *Batrachosuchus watsoni* (Haughton, 1925) a depression in the vomer is indicated by Watson (1956) and Welles and Estes (1969), but this depression is more posterior than the foramen found in *B. browni.* This foramen probably housed a gland. It is roughly triangular with the apex pointing posteriorly. The base is 9 mm across and the midline length is 9 mm.

The matrix has not been removed from the subtemporal vacuities, due to the delicacy of the surrounding bones and the overlying skull roof.

Vomers. The most anterior limits of the vomers are not preserved. In the anterolateral corner of each vomer, a large tusk next to a tusk depression is present. Posterolateral to the tusk the suture with the palatine is interrupted by the choana. From the posteromedial corner of the choana the suture with the palatine slants posteromedially to the anterolateral corner of the interpterygoid vacuity. The posterior ends of the vomers project on either side of the cultriform process of the parasphenoid. There is no depression in this area as in *Batrachosuchus watsoni,* but the two elements blend smoothly together.

Palatine. The most anterior limits of the palatine are not preserved. Posterolateral to the choana is a large tusk adjoining a broken tusk base and further posterolaterally to this pair of tusks the sinuous anterolaterally directed suture with the ectopterygoid is visible extending to the anterolateral corner of the interpterygoid vacuity.

Ectopterygoid. The anterolateral limits of the ectopterygoid are not preserved. Two teeth (tusks) smaller than the vomerine and palatine tusks are present just lateral to the anterolateral corner of the interpterygoid vacuity. Posteriorly, an interdigitated almost straight transverse suture with the pterygoid enters the anterolateral border of the interpterygoid vacuity.

Parasphenoid. The parasphenoid forms a large polygonal body underlying the exoccipitals posteriorly and the pterygoids laterally. The body is smooth and slightly concave. Two grooves following the lateral margins of the cultriform process extend into the body, at the centre of which is a very shallow transverse depression which is probably homologous with the *crista muscularis* of the capitosaurs. The cultriform process narrows from 4,2 cm at its base to 1,9 cm almost halfway along its length. The process then broadens to 2,5 cm at its anterolateral sutures with the vomers. The parasphenoid does not extend to the posterior limit of the skull as it does in *Batrachosuchus watsoni* but leaves a gap of 1 cm from this border. The quadrate is missing.

Pterygoid. The pterygoid displays the typical condition found in the brachyopids in that the lateral edge of the palatine flange turns through 90 ° forming the vertical inner wall of the subtemporal vacuity. Posterolaterally, the pterygoid sutures with the exoccipital on an almost straight posterolaterally directed line. The quadrate ramus of the pterygoid is expanded so that the posterolateral corner of the vertical flange lies 1,2 cm posterior to the edge of the palatal portion.

In occipital view the pterygoid sutures medially with the exoccipital in a dorsolaterally slanted suture. It then extends laterally forming the ventral border of the otic recess before turning vertically. A part of the parotic plate of the pterygoid is visible on the dorsolateral surface of the pterygoid (as in *Batrachosuchus watsoni*, illustrated by Watson, 1956).

Choanae. The right choana measures 1,8 cm at its narrowest breadth by 2,6 cm at its long axis. The anterior limits of the left choana are not preserved and the shape seems to be distorted. The right choana has its long axis transverse to the midline.

Interpterygoid vacuity. The interpterygoid vacuity has its greatest width along its anterior border. The right measures 6,1 cm at its anterior border by 10 cm; the left measures 5,6 cm at its anterior border by 10 cm, this discrepancy being due to distortion.

Subtemporal vacuity. The subtemporal vacuity is obscured by matrix which, if removed, may endanger the skull roof. Its inner border is formed by the vertical flange of the pterygoid.

Discussion

When comparing *B. browni* to *B. watsoni* confusion is encountered (see table 6) as the three existing sets of plates and illustrations of *B. watsoni* show different skull proportions; e.g. in Watson's (1919) plate which is "½ approximately", the skull length is 19,2 cm, whereas in Watson's 1956 reconstruction the skull length is 16 cm. In Welles and Estes (1969) their new reconstruction of the skull length is only 11,5 cm, but this is taken from new casts provided by the British Museum of Natural History and probably provides the most reliable information. However, when comparing the plate in Watson (1919) to *B. browni* as now reconstructed, the two skulls look very similar and the possibility exists that they are of the same species. This would explain away the inconsistency of there being two sympatric species of brachyopid in the same horizon (*Cynognathus* zone). Excluding the general skull morphology which is difficult to assess for reasons already given, there are supposedly four main differences; these are:

(1) the presence of an interfrontal in *B. browni*;
(2) the presence of a vomerine foramen in *B. browni*;
(3) the parasphenoid does not reach the edge of the palate as it does in *B. watsoni*;
(4) the wider lateral line canals of *B. watsoni* and their distribution.

Looking at the plate of *B. watsoni*, the area where an interfrontal would be found is rather unclear but it seems that there is a possibility that sutures of an interfrontal are in fact discernible. This point could be resolved with microscopic examination of the area.

Considering Watson's (1919) plate showing the palate, in the position of the vomerine foramen found in *B. browni*, a distinctly triangular depression is visible. Although Welles and Estes (1969) describe the area as a depression perhaps further preparation, if possible in this area, would uncover a foramen in *B. watsoni*.

The parasphenoid of *B. watsoni* may not reach the edge of the palate. In Watson's (1919) plate there seems to be a suture running just anterior to that margin. The wider lateral line canals could be due to a lateral compression which widened the canals, or *B. watsoni* may be a young indivudal and perhaps the lateral line canals would close together as the animal got older. The variation of their distribution may also be due to sexual dimorphism or individual variation. However, there is no evidence as yet available to verify these theories and as the wider lateral line canals of *B. watsoni* could have been an adaptation to faster-flowing water speciation may well have occurred even though the two localities are approximately 56 km apart.

Thus, until these four characters are explained away, it seems advisable to retain the two South African species and Welles and Estes (1969) indices are used by the author for comparisons.

One further factor which emerged from discussion and which may have a bearing on the relationships and function of the three Southern African members of the genus *Batrachosuchus* is the degree to which the occipital condyles protrude behind the skull roof. Measured on the dorsal surface this character is greatest in *B. watsoni* (29 %), less so in *B. browni* (20 %), and is very much reduced in *B. concordi* (< 5 %). Thus the last-named species has a reduced ability to raise the upper jaw for mouth-opening and hence, by implication, there is a requirement for the skull to be kept well clear of the ground so as to allow the lower jaw sufficient movement to clear the palatal fangs. This also would require relatively robust forelimbs and pectoral girdle to support the body; this requirement is met in the well-ossified bones described from the post-cranial remains.

By comprison the other two species would appear well suited to a greater degree to a bottom-living, aquatic existence where mouth-opening movements would be effected by a combination of powerful nuchal and *depressor mandibuli* muscles. A comparison of the anterior vertebrae of these forms with the axis and atlas of *B. concordi* would be of great value here, as would a knowledge of their limb morphologies. In this case *B. browni* seems less well adapted to the bottom-dwelling habit which, with the difference in development of the lateral line canals when compared with *B. watsoni*, might help explain the presence of these two closely related species in the *Cynognathus* zone, *B. watsoni* being a permanent dweller in swift-flowing waters and *B. browni* perhaps preferring more transient waters.

In this case it is interesting to note that *B. concordi* might show an unusual reversal of the normal evolutionary trends of the temnospondyls in seemingly being less well-adapted to an aquatic environment. If the age of the N'tawere Formation is the same as the *Cynognathus* zone (and the large geographical separation of the two not significant) then the three species would occupy three separate niches in river ecology. If, as is more likely, the N'tawere Formation is the younger of the two, then an evolutionary sequence within the genus *Batrachosuchus* can be demonstrated based on this one character.

SUMMARY AND CONCLUSIONS

1. The family Brachyopidae, which in South Africa is part of the *Cynognathus* zone fauna of the Beaufort series, may be defined as: labyrinthodonts; orbits large; palate ∩-shaped; retroarticular process long; skull outline more or less parabolic; occipital condyles project far behind the posterior edge of skull roof; no zones of relative intensive growth; basicranial joints absent; pterygoids joined by suture to parasphenoid; palatal teeth present on vomer and palatine.
2. Only one genus *Batrachosuchus* is represented in Southern Africa by three species: *B. browni* and *B. watsoni* from the *Cynognathus* zone of South Africa and *B. concordi* from the N'tawere Formation in the Upper Luangwa Valley, Zambia. The genus may be defined as brachyopids with broad parabolic skulls; orbits far forward; postorbital part of skull very long; narrow internarial width; lateral line grooves well defined; extension of supraorbital lateral line canal onto parietal bone.
3. *B. watsoni* may be defined as a large *Batrachosuchus;* skull broader than that of *B. browni;* greater internarial width; greater interorbital breadth; longer preorbital region; shorter orbits; longer postorbital deck; lateral line canals well defined and broad; parasphenoid reaches limit of skull base; depression in centre of vomer; one lateral line canal present on postfrontal.
4. *B. browni* may be defined as a large *Batrachosuchus*; skull relatively narrower than that of *B. watsoni*; narrower interorbital breadth; shorter preorbital region; longer orbits; shorter postorbital deck; lateral line canals well defined, but relatively much narrower and of more ∩-shape in section than in *B. watsoni*; parasphenoid does not reach skull limit; vomerine foramen in centre of vomer; 3 lateral line canals present on postfrontal; evidence of paired tusks on vomer, palatine and ectopterygoid.
5. *B. concordi* may be defined as a small *Batrachosuchus* with a skull narrower than *B. browni* and much narrower than *B. watsoni*; interorbital breadth very much narrower than both *B. browni* and *B. watsoni*; shorter preorbital length than *B. browni*, much shorter than *B. watsoni*; orbit slightly smaller than *B. browni*; postorbital length greater than *B. browni*, but shorter than *B. watsoni*; interpterygoid vacuity shorter than *B. browni* and much shorter than *B. watsoni*; interpterygoid vacuity narrower than both *B. watsoni* and *B. browni*; distance of parietal foramen from posterior of skull table greater than both *B. browni* and *B. watsoni*; lateral line canals weakly defined; parasphenoid reaches limit of skull; exoccipital

TABLE 6

Differences in Measurements of the Three Illustrations of *Batrachosuchus watsoni*

	Watson 1919 cm	Watson 1956 cm	Welles and Estes 1969 cm
Interorbital breadth, A	9,8	7,2	5,0
Breadth of skull roof across quadratojugals, B	27,5	18,5	16,5
Midline postorbital length, D	12,2	10,0	7,0
Midline distance between nostrils and orbits, F	2,2	1,4	1,0
Height of parasphenoid, H	—	4,2	3,5
Internarial breadth, J	2,0	1,5	1,1
Length of skull roof, L	19,2	16,0	11,5
Midline preorbital length, O	4,4	2,7	2,4
Distance behind orbits of parietal foramen, P	6,0	5,0	3,3
Length of body of pterygoid, Q	5,0	3,8	3,4
Breadth across pterygoids at concavity, R	20,8	12,4	11,2
Distance of parietal foramen in front of end skull table, T	4,8	4,0	3,0
Breadth of snout 1/5th of skull length from tip, S	17,4	10,8	9,2
Midline orbital length, U	3,8	3,3	2,5
Length of interpterygoid, Y	10,4	7,2	5,7
Breadth of interpterygoid, Z	6,0	4,0	3,3
Distance of exoccipital behind skull table	5,0	2,2	2,0

does not project as far posteriorly as in either *B. browni* or *B. watsoni*; in addition a lingual process of the angular is present (the jaws of the other two species of *Batrachosuchus* are unknown).

6. *B. concordi* is more or less on the same evolutionary level as the *Cynognathus* zone brachyopids, in agreement with other evidence that the N'tawere Formation is probably of a similar age, and probably Early Middle Triassic (Chernin and Cosgriff, 1975).

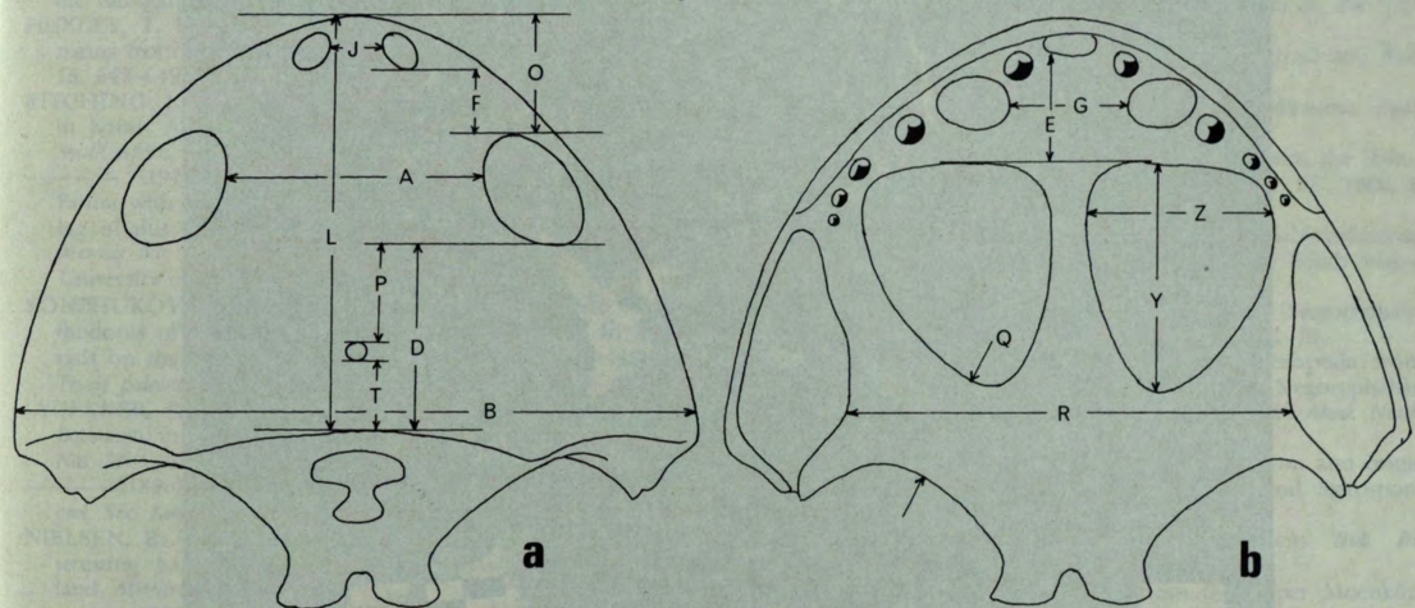

Figure 6. Diagrams of brachyopid skull showing measurements of dorsal surface and palate from Welles and Estes (1969, fig. 1, p. 5).

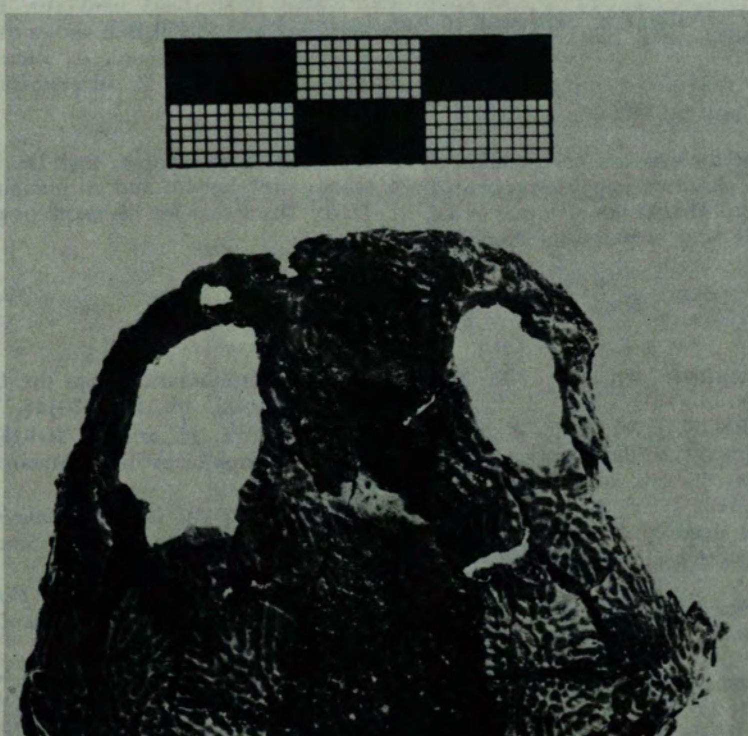

Figure 7. The skull of *Batrachosuchus concordi* dorsal view.

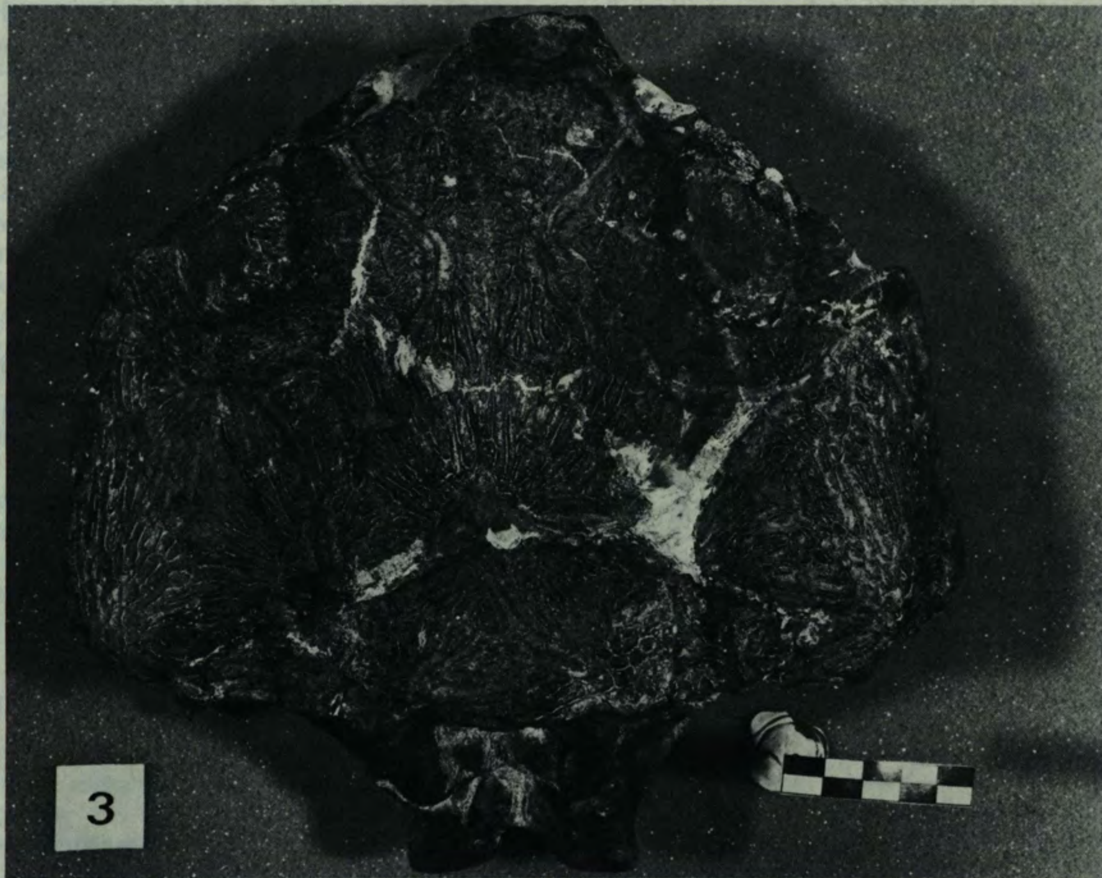

Figure 8. The skull of *Batrachosuchus browni* dorsal view.

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LIST OF ABBREVIATIONS

a — angular
art — articular
bac — basioccipital chamber
bas — basal process
c — coronoid
ch — choana
cm — crista muscularis
con — condyle
cp — cultriform process
d — dentary
dor — dorsal process
ec — ectopterygoid
eo — exoccipital
epi — epipterygoid
f — frontal
fad — adductor fossa
fm — foramen magnum
fma — anterior meckelian foramen
fmp — posterior meckelian foramen
fogl — glenoid fossa
fpsym — postsymphsial foramen
ic — intercoronoid
if — interfrontal
inl — infraorbital canal
iv — interpterygoid vacuity
j — jugal
la — lacrimal
mx — maxilla
n — nasal
nr — nare
ot.r — otic recess
p — parietal
paf — paraquadrate foramen
pal — palatine
palt — palatine tusk
par — paroccipital process
par. ot. pr. — parotic part of pterygoid as far as exposed
pc — precoronoid
pf — postfrontal
pmx — premaxilla
por — postorbital
pos — postsplenial
pp — postparietal
ppt — palatine ramus of pterygoid
pra — prearticular
pref — premaxillary foramen
prf — prefrontal
prprc — precondylar process
prptc — postcondylar process
ps — parasphenoid
ptf — posttemporal fossa
q — quadrate
qj — quadratojugal
qpt — quadrate ramus of pterygoid
rp — retroarticular process
sa — surangular
sf — subtemporal vacuity
sp — splenial
sq — squamosal
stp — supratemporal
sul — supraorbital canal
sym — symphysis
t — tabular
tl — temporal canal
v — vomer
ven — ventral process
vf — vomerine foramen