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Southern African Triassic Labyrinthodonts: the Capitosauridae and the Brachyopidae

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similarity that Welles and Estes (op. cit.) exclude it from the Brachyopidae.

Enosuchus breviceps, Efremov (in Konjukova), 1955 from the Russian Zone II (Late Permian) of the Isheevo site in the Tatar A.S.S.R. It is excluded from the Brachyopidae because even though the skull is short and broad, the contact of parietal and tabular is anthrachosaurian rather than temnospondyl and the shape of the tabulars is very different from any of the brachyopids.

Plagiorophus paraboliceps, Konjukova (1955) from the Early Triassic Zone V of Chkalov province, U.S.S.R. The genus and species was based upon a fragment of quadrate and quadratojugal. The exceptional feature is the extreme lateral projection of the quadratojugal which is indicative of a broad skull, and yet is not brachyopid as the quadratojugal of brachyopids is reduced to a thin plate below the squamosal.

Eobrachyops townendae Watson, 1956 from the Upper Permian Clear Fork beds of Texas. The valid name for this specimen is Isodectes megalops (Cope, 1883) although it has been successively called Pariotichus megalops Cope, Trimerorhachis conangulus Cope, Acheloma ? casei Broili and Eobrachyops townendae, Watson. It seems that this form is best classified within the Superfamily Trimerorachoidea in a family separate from Trimerorachidae and the Saurerpetontidae.

Indobrachyops panchetensis, Huene and Sahni, 1958 from the upper Panchet rocks (Early Triassic) of India. Although Indobrachyops has a short broad skull and short, wide tabular, it lacks the arched palate, broadened pterygoid and the ectopterygoid tusks of true brachyopids.

Cosgriff (1969) remarked on the problematic species as follows:

"Tungussogyrinus bergi: Positive assignment is impossible. The construction of the quadrate region, crucial for comparisons with the Brachyopidae is unknown." The skull apparently lacks the high vault of the posterior part of the palate which is characteristic of the brachyopids, and the exceptionally broad cultriform process with the solid, elongate vertebral centra suggest the Plagiosauria.

Indobrachyops panchetensis: The rudimentary otic notch is similar to that in Brachyopidae, but in other respects the Indian species is quite different. The exoccipital condyles lie closer to the posterior margin of the skull roof. The cheek region is shallow and the peculiar brachyopid modifications of the pterygoid, squamosal and quadratojugal are not present.

The sculpture of Indobrachyops consists of irregular vermiculose ridges and bears little resemblance to either the lineate sculpture of Dvinosaurus or the reticulate pattern of the Brachyopidae. The skull, although broad and short has a different shape from a brachyopid skull. The brachyopid skull has a bulging cheek region and the greatest width of the skull lies anterior to the posterior corners. Indobrachyops has straight cheek margins and the greatest width lies at the posterior corners.

Tupilakosaurus heilmani: Shishkin (1961) concluded that the skull fragment of T. heilmani was derived from a broad-skulled labyrinthodont of the superfamily Brachyopoidea. He made the genus the type of a new family, Tupilakosauridae and accepted embolomerous vertebrae found scattered in the same shale slab as derived from the same skeleton as the skull fragments. Nielsen (1967) accomplished further preparation on the shale slab and found that the dorsal aspect of the skull fragment confirms its brachyopid nature but is too incomplete by itself for extensive comparisons with other species of the superfamily.

Tupilakosaurus wetlugensis: The generic assignment rests on the similarity of the central elements to those preserved on the shale slab with the indeterminate skull fragments of T. heilmani. The association of such vertebrae with a temnospondylous skull is as suspect in this case as it is in the Greenland occurrence. Shishkin (1961) does not indicate whether the vertebrae were found articulated with the skull or even in close proximity to it. Also, the occurrence of embolomerous vertebrae in a brachyopid would be anomalous as all members of the superfamily for which vertebral structures are known are temnospondylous. Large, wedge-shaped intercentra occur in Dvinosaurus primus (Bystrow, 1935). Many features of the skull of T. wetlugensis closely resemble those of Dvinosaurus primus. The anterior end of the cultriform process has a pronounced expansion between the enclosing wings of the vomers in T. wetlugensis as in D. primus. Both genera possess vestiges of a palatal tooth row. The arrangement of bones and lateral line grooves on the dorsal surfaces of the skulls is very similar in the two genera. The parietal bones have lateral borders on the postorbital bones in the T. wetlugensis skull and in one specimen of D. primus. The orbits in both genera are spaced moderately far apart. The most notable difference between T. wetlugensis and D. primus is in the structure of the basicranial region of the palate. D. primus possesses the movable joints of the central parasphenoid-basisphenoid complex with the lateral pterygoid bones found in

Eobrachyops and other Early Permian genera, but in T. wetlugensis the parasphenoid is solidly fused to the pterygoids. If T. wetlugensis is a Triassic descendant of the Late Permian Dvinosaurus then this lineage has paralleled that of the brachyopids and other labyrinthodont families in the loss of the basipterygoid joints.

The species retained in the Brachyopidae are:

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). The material is very poor. However, the characteristic straight occipital border and the absence of otic notches are certain. The lateral line grooves are relatively narrow. In side view it is evident that the hinder part of the maxilla lower border is turned a little downward, the lower border of the jugal and quadratojugal continuing the trend. Length of skull table approximately 11 cm; breadth of skull across quadrates approximately 13 cm.

Welles and Estes (1969) attempted a new reconstruction of Brachyops, based on all previous illustrations plus a restudy of the original specimen. This was done as the authors considered this specimen not only the type of the species, but the species is the type of the genus and in turn the subfamily, family and order were based upon this specimen. They state: (op. cit.)

"The surface sculpture is worn and eroded but indicates a strongly linear pattern rather than a reticulate network. The premaxilla extends about 1.4 cms around the snout to meet the maxilla beneath the external naris. It is overlapped internally by the vomer and forms the anterior border of the anterior palatal vacuity. The vomers form a broad plate, their posterior tips extend about 4 cms behind the anterior pterygoid vacuity to underlie the parasphenoid considerably behind the anterior border of the interpterygoid vacuity. There seem to be two vomerine tusks, one near the anterior palatal vacuity and the other near the choana. The parasphenoid has a large, flat body that underlies the exoccipital nearly to the condyle. Its cultriform process narrows to 0.6 cms between the interpterygoid vacuities, and broadens to 1.1 cm at the vomerine contact. The exoccipital forms a very small part of the palatal surface, being almost entirely overlapped by the parasphenoid. It extends anterolaterally about 1.1 cm from the edge of the condyle, to meet the

pterygoid. The palatine forms the posterolateral border of the choana and extends back inside the maxilla to meet the ectopterygoid. A single relatively enormous tusk, 2.2 cm long is situated just behind each choana. The pterygoid has the peculiar brachyopid form with a great downturned lateral flange that extends back beyond the quadrate. The quadrate ramus slopes 73 degrees from the horizontal and is a narrow plate 0,9 cm broad. The palatine ramus is 1.1 cm broad. The anterior palatal vacuity is approximately 1,5 cm from the choana and is 1.4 cm in transverse breadth. The choana is 0,9 cm anteroposteriorly and 1.2 cm transversely, much larger relative to skull size than in other brachyopids. The interpterygoid vacuity is widest at the front. The subtemporal vacuity lies entirely behind the orbit and opens ventrolaterally."

Thus a composite definition of Brachyops laticeps Owen 1855 could be: a small brachyopid with a parabolic skull; snout tapered to a 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 linear patterned.

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. The anterior part of the skull is very depressed while the occipital border is very deep. Welles and Estes (1969) state that Bothriceps differs from Brachyops in fundamental skull proportions. In relation to skull length, it is very narrow; the nares are closer together; the orbits are very much closer together; the preorbital region is extremely long; the orbits are slightly longer, and the postorbital deck is very short. Relative to interorbital breadth, the parietal foramen is a little closer to the orbits, but very far from the back of the deck. These differences are so great and so diverse in their nature that Bothriceps, though a brachyopid, is quite apart from Brachyops and its relatives.

Cosgriff (1969) states that the skull has a slightly pointed snout tip which gives the dorsal aspect a triangular outline. The orbits are large and closely spaced and are set relatively farther back on the skull roof; the preorbital length of the skull roof is 33% of the total midlength of the skull roof. Each interpterygoid vacuity is more or less semicircular. The

broad subtemporal fossa is indented on its medial margin by a projection of the pterygoid bone.

Thus, a composite definition of Bothriceps australis could be: a small brachyopid with a 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.

Blinasaurus wilkinsoni Cosgriff, 1969

Platyceps wilkinsoni (Stephens, 1887)

Proc. Linn. Soc. N.S.W., 2, 1175-1195

Bothriceps wilkinsoni (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, Narrabern Group, (Middle Triassic).

Watson (1956) interpreted the animal as neotenous although the small size (skull length about 2.7 cm) may support Stephens (1887) and Romer's (1947) contention that the specimen was a larval form, possibly of Bothriceps. Lydekker (1890) referred this genus to Bothriceps. Welles and Estes (1969) state that compared to Brachyops and relative to skull length, the skull is extremely narrow. In relation of interorbital breadth, the parietal foramen is very close to the orbits and extremely far in front of the posterior end of the skull. Welles and Estes (op. cit.) conclude that in general it is so like Bothriceps that on the basis of published information they consider that the two are congeneric.

Cosgriff (1969) states that strictly definitive characters to distinguish Blinasaurus from the other genera of the family are entirely lacking, necessitating a differential diagnosis as follows:

"Bothriceps and Trucheosaurus: The skull roof is roughly triangular in dorsal view whereas that of Blinasaurus is nearly circular. The antorbital portions of the skull roofs are relatively longer.

Brachyops: The snout is slightly pointed in dorsal view; in Blinasaurus it is evenly rounded. The orbits are more widely spaced.

Batrachosuchus: The orbits are more widely spaced than in Blinasaurus. The supraorbital canals of the lateral line system extend back onto the parietal and supratemporal bones and are not joined to the infraorbital and temporal canals on the postorbital bones as in Blinasaurus.

Boreosaurus: The adductor fossa of the lower jaw is comparatively smaller than in Blinasaurus.

Hadrokkosaurus: The adductor fossa of the lower jaw is comparatively smaller than in Blinasaurus. The labial surface of the lower jaw is devoid of the sculpture as present on Blinasaurus, but contains a lateral mandibular fenestra absent in Blinasaurus."

Cosgriff (1969) defines Blinasaurus wilkinsoni (Stephens 1887) as follows:

"The orbits are relatively smaller than those of Blinasaurus henwoodi; the orbital length as measured on the midline is only about a quarter of the midline length of the skull roof whereas in B. henwoodi it is nearly one third. The parietal and postorbital bones are in sutural contact whereas in B. henwoodi they are separated by a sutural contact of the postfrontal and supratemporal bones. The frontal bone is separated from the medial margin of the orbit, whereas in B. henwoodi the frontal bone forms part of the medial margin". Thus, a composite definition of Blinasaurus wilkinsoni could be: a very small brachyopid with a narrow parabolic skull; orbits close together; parietal foramen very close to orbits; in dorsal view skull roof nearly circular.

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.

Cosgriff (1969) defines this species as follows: "The orbits are relatively larger than those of B. wilkinsoni. The parietal bone is separated from the postorbital bone by a postfrontal-supratemporal suture whereas in B. wilkinsoni they are in sutural contact. The frontal bone forms part of the medial margin of the orbit, whereas in B. wilkinsoni it is excluded from this margin by a prefrontal-postfrontal suture".

Thus a composite definition of Blinasaurus henwoodi could be: a small brachyopid with a narrow parabolic skull; orbits close together; parietal bone separated from postorbital bone by a postfrontal-supratemporal suture; frontal forms part of the medial margin of orbit.

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 B.M.N.H. as 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) commented on the portion in the British Museum. This consists of two blocks, one contains the ventral impression of the skull roof and the other 28 vertebrae with articulated ribs and also a few limb bones.

Watson (1956) redescribed and reillustrated B.M.N.H. No. R3728 and placed the species in a new genus Trucheosaurus. Welles and Estes (1969) state that the differences of this specimen from Brachyops and Batrachosuchus are of the very same nature and of almost exactly the same magnitude, as those shown by Bothriceps australis, except for relative size of the orbit. Its resemblances to the latter are so pronounced that, except for the longer tabulars, it might be considered as an individual variant. Welles and Estes (1969) contend that separation at the specific level could be justified, but the erection of a new genus is not necessary on the present evidence, so they returned it to the genus Bothriceps.

Cosgriff (1969) retains the name Trucheosaurus major for this specimen. After studying N.S.W.G.S. No. F12697 he described a few characters as follows: "The tip of the snout of T. major is slightly pointed and the triangular outline of the skull closely matches that of B. australis. The preorbital portion of the skull is as long as in B. australis, being 34% of the total skull roof midline length. The orbits, however, are relatively smaller and more widely spaced than in B. australis, or in the species of Blinasaurus. The orbit length is 20% of the total skull midline length and the least interorbital width is 46% of this measurement".

Thus, a composite definition of Trucheosaurus major could be: large brachyopid with a skull roughly triangular in dorsal view; preorbital

length of skull 34% of skull length; orbits relatively smaller and more widely spaced than in B. australis; orbit length 20% of total skull length; tabulars longer than in B. australis.

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. Haughton provided the species name Batrachosuchus watsoni.

Welles and Estes (1969) state that it is close to B. browni. The main differences relative to skull length are: "very much broader skull than in B. browni, narrow internarial area, greater interorbital breadth, longer preorbital region, shorter orbits and longer postorbital deck, longer body of pterygoid and broader interpterygoid vacuity". Welles and Estes (1969) conclude that the differences are at least of specific degree and might even justify erection of a new genus; however, for the present they consider B. watsoni as a more advanced species with a much broader skull than B. browni.

Cosgriff (1969) states that three features of the skull indicate that this species is more closely related to the species of Blinasaurus than is Bothriceps australis, Trucheosaurus major and Brachyops laticeps. "The snout region has a broadly parabolic outline in dorsal view as in the species of Blinasaurus and not slightly pointed as in other species. The subtemporal fossae are long and narrow as in Blinasaurus henwoodi and lack the medial indentations formed by projecting processes of the pterygoids observed in Bothriceps australis. The level of the quadrate condyles is far anterior to the level of the exoccipital condyles as in both species of Blinasaurus, whereas in Bothriceps australis the quadrate and exoccipital condyles are nearly on the same hinge line. Each of the exoccipital-pterygoid sutures visible on the palatal surface of the Batrachosuchus watsoni skull is nearly 2 cm in length and in this respect also the species is much closer to Blinasaurus henwoodi than it is to Bothriceps australis. The principal features that distinguish Batrachosuchus watsoni from the species of Blinasaurus are the position of the orbits on the skull roof and the arrangement of the canals of the lateral line system. In regard to the lateral line system, the major difference between Batrachosuchus watsoni and the species of Blinasaurus is the course of the supraorbital canal in the postorbital region. This canal, in Batrachosuchus watsoni does not

join the infraorbital and temporal canals in the postorbital bone. Instead, it curves medially behind the level of the posterior border of the orbit and ends blindly in the parietal bone. The species of Blinasaurus, however, resembles Bothriceps australis, Brachyops laticeps and most other temnospondyl species in possessing confluences of supraorbital, infraorbital and temporal canals in the postorbital bones. A number of features of the palatal surface distinguish Batrachosuchus watsoni from Blinasaurus henwoodi. The interpterygoid vacuities are relatively smaller with a distinctive outline. The anterolateral 'corner' of each vacuity is on the same level as the anteromedial 'corner', whereas in Blinasaurus henwoodi the anterolateral 'corner' is posterior to the anteromedial 'corner'. The cultriform process lacks a waist in the centre of its length. The vomerine tusks are considerably smaller than the palatine tusks and not equal to them in size as in Blinasaurus henwoodi."

Thus a composite definition of Batrachosuchus watsoni could be: a large brachyopid with a broadly parabolic skull outline; orbits far forward; postorbital part of skull very long; interpterygoid vacuity very short; narrow internarial area; lateral line grooves well defined and broad.

Batrachosuchus lacer (Shishkin, 1966)

(Batrachosuchoides lacer Shishkin, 1966)

This species is based upon the anterior part of the 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. Thus although these fragments illustrate some interesting osteological details, they are not sufficiently complete for a specific diagnosis. In the index of internarial breadth to interorbital breadth, this specimen is nearer to Batrachosuchus watsoni than to B. browni. In the F : A index (nares to orbits, sagittal distance; interorbital breadth) it shows a closest relationship to Hadrokkosaurus bradyi, with Batrachosuchus browni

and B. watsoni next in order respectively". Welles and Estes (1969) draw no conclusions from these few data, but as yet find no reason to exclude the Viatki brachyopid from the genus Batrachosuchus.

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 holotype, 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 six miles west of Holbrook, Arizona (probably Lower-Middle Triassic).

Welles and Estes (1969) diagnose the species as follows: "An extremely large brachyopid (length of skull approximately 23,4 cm). Relative to skull length, nares extremely far apart; orbits extremely far apart. Relative to interorbital breadth, parietal foramen close behind orbits. Interpterygoid vacuity extremely broad in relation to its own length. Dermal sculpture of radiating ridges, sensory canals nearly obliterated. Quadrate ramus of pterygoid a vertical plate projecting far behind squamosal. Lower jaw smooth-surfaced, with retroarticular process one-fourth of total jaw length; adductor fossa equally long. Dentary teeth set in broad, shallow groove, with bulbous bases that shed with tooth. Tooth row very short, only about half the jaw length".

Cosgriff (1969) commented on Hadrokkosaurus bradyi as follows: " In labial view the ventral edge of the jaw is bowed slightly upward under the tooth row and again under the articular facet. The lingual wall of the adductor fossa is much lower than the labial wall. The posterior meckelian foramen and angular-prearticular suture, although not on the ventral surface are placed very low on the lingual surface. Two features of the labial surface of the lower jaw are unique to Hadrokkosaurus bradyi among the Brachyopidae: the external surfaces are devoid of sculpture; and a large lateral mandibular fenestra is present between the dentary and surangular bones. Hadrokkosaurus bradyi is also distinguished from Blinasaurus henwoodi by the same features which distinguish Boreosaurus thorslundi: the adductor fossa is relatively shorter and the posterior meckelian foramen is relatively larger".

Thus a composite definition of Hadrokkosaurus bradyi could be: An extremely large brachyopid with a 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.

Boreosaurus thorslundi Nilsson, 1943

The material included in this taxon by Nilsson, consists entirely of lower jaw fragments from the Sticky Keep Formation of Spitzbergen (Lower Triassic). As already noted, Welles and Estes (1969) exclude this genus from the Brachyopidae because of the very short retroarticular process.

Cosgriff (1969) however, includes this species in the Brachyopidae and comments as follows:"Boreosaurus thorslundi is a brachyopid as Nilsson believed and a brachyopid as listed by Romer (1966). As in Dvinosaurus primus and Bothriceps australis, the posterior meckelian foramen and the angular-prearticular suture are located low on the lingual surface. Two details of construction provide evidence for the referral of Boreosaurus thorslundi to the Brachyopidae. The adductor fossa is long and narrow and the entire jaw is very slender, specifically recalling the jaws of Blinasaurus henwoodi rather than those of Dvinosaurus primus. Impressions of reticulate sculpture associated with the paratypes of Boreosaurus thorslundi lend circumstancial support for this assignment. The retroarticular process of the holotype, broken off close to its base, was probably elongate as in other brachyopids rather than short and knob-like as in Dvinosaurus primus. One feature of lower jaw construction indicates closer relationship of Boreosaurus thorslundi to the Lower Triassic Blinasaurus henwoodi than to the Upper Permian Bothriceps australis. The entire jaw ramus is bowed strongly upward in lingual view whereas in Bothriceps australis it is nearly straight from the symphysis to the region beneath the articular facet. The comparatively large size of the adductor fossa of Blinasaurus henwoodi is the principal feature of this species distinguishing it from Boreosaurus thorslundi. The labial wall of the fossa is much higher in Blinasaurus henwoodi than it is in Boreosaurus thorslundi. The posterior meckelian foramen and angular-prearticular suture lie closer to the ventral edge of the jaw in Blinasaurus henwoodi than in Boreosaurus thorslundi. The posterior meckelian foramen of Blinasaurus henwoodi is relatively smaller".

Thus a composite definition of Boreosaurus thorslundi could be: 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.

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 Q6

Duckworth Creek, South Central Queensland. The horizon is the Lower Upper Rewan Formation of the Mimosa Group. (Lower Triassic). It differs from Brachyops laticeps especially in that its exoccipital condyles are much nearer the level of the quadrate condyles so that the backwardly sloping portion of the occiput in B. allos is greatly reduced. The cultriform process of the parasphenoid in B. allos is clasped laterally by posteriorly directed processes of the vomers rather than being overlain by them as is the case in B. laticeps. Posteromedially, the process bears an area of dermal denticles in B. allos. On the dorsal surface of the skull the tabulars are exposed a little less in B. allos, than they are in B. laticeps. Anteriorly the interpterygoid vacuities are broader in B. allos, but this difference is less between B. allos and B. laticeps than between B. allos and all other brachyopids. The rather long tripartite anterior palatal foramen in B. allos is also distinctive.

Although the special character of the exoccipital condyles being nearer the level of the quadrate condyles is considered by Watson (1956) to be critical in showing the stage of evolutionary advancement in brachyopids, the two species are otherwise so alike that generic separation at this stage is inadvisable.

Thus, a composite definition of Brachyops allos could be: with a 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.

Notobrachyops picketti Cosgriff, 1973

This specimen (New South Wales Geological Survey No. F8258) 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). The skull roof is relatively narrow, greatest skull width across quadratojugal bones approximately nine-tenths of skull sagittal length. The antorbital portion of the skull roof is relatively long as in Bothriceps australis; the skull roof anterior to the

orbits is approximately one-third of the skull sagittal length. The orbits are set close together as in Bothriceps australis, Blinasaurus wilkinsoni and Blinasaurus henwoodi; the least interorbital width is approximately three-tenths of skull sagittal length. Each bone element of the skull roof is elevated in the central region and depressed around sutural edges, producing an undulating surface over the entire skull roof. The posterior edge of the skull roof is strongly convex and evenly curved between otic embayments.

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

Austrobrachyops jenseni Colbert and Cosgriff, 1974

This species was based on a left pterygoid bone more or less intact (American Museum of Natural History No. 9346) and a referred fragment of lower jaw (A.M.N.H. No. 9301). The fragments were found in the Coalsack Bluff, Transantarctic Mountains. The horizon is the lower part of the Fremouw Formation (Lower Triassic).

This is a brachyopid in which the posterior edge of the ascending ramus of the pterygoid bone possesses a distinct angle in the middle of its course, giving the stapedial fossa a quadrangular shape. This angle on the ascending ramus is surmounted by a longitudinal suprapterygoid crest. The ventro-lateral corner of the stapedial fossa is incised by a groove for the internal carotid artery. The posterior border of the pterygoid corpus is diagonal to the skull midline.

As regards the lower jaw fragment, closest relationships lie with ?Batrachosuchus (Watson, 1956, Fig. 9), Batrachosuchus, and Blinasaurus henwoodi. In each of these, as in A.M.N.H. 9301, the labial wall of the adductor fossa is considerably higher than the lingual wall and the retroarticular process, as measured along its dorsal surface, is approximately three times the antero-posterior length of the articular facet. Surface sculpture and lateral line grooves of the labial surface serve to distinguish A.M.N.H. 9301 from the various jaw fragments referred to Batrachosuchus. The sculpture on the Antarctic specimen consists of elongate pits, whereas in the South African specimens, it is composed of rather regular ridges and grooves that run longitudinally across the labial surface.

The oral and mandibular grooves, well marked on the Antarctic specimen, are lacking on those from South Africa. Sculpture and lateral line grooves are not well preserved in Blinasaurus henwoodi and hence, the affinities of this species in these respects cannot be determined. The lower jaws of Hadrokkosaurus bradyi contrast with those of the other forms in the height of the labial wall of the adductor fossa and in the relative length of the retroarticular process. In Hadrokkosaurus bradyi the labial wall of the fossa is only slightly higher than the lingual wall, but the retroarticular process is proportionally very long, approximately six times the anteroposterior length of the articular facet. Also, surface sculpture is poorly developed on the labial surface and there are no traces of the lateral line grooves.

Thus a composite definition of Austrobrachyops jenseni could be defined as follows: a brachyopid in which the pterygoid bone possesses a distinct angle in the middle of its course; ventro-lateral 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.

To summarise: at present 13 species of brachyopids are recognised ranging in time from the Upper Permian to Upper Triassic. They are:

Trucheosaurus major	-	Upper Permian
Bothriceps australis	-	Upper Permian
Brachyops laticeps	-	Uppermost Permian
Blinasaurus henwoodi	-	Lower Triassic
Austrobrachyops jenseni	-	Lower Triassic
Brachyops allos	-	Lower Triassic
Batrachosuchus lacer	-	Lower Triassic
Boreosaurus thorslundi	-	Lower Triassic
Batrachosuchus watsoni	-	Lower-Middle Triassic
Batrachosuchus browni	-	Lower-Middle Triassic
Hadrokkosaurus bradyi	-	Middle Triassic
Blinasaurus wilkinsoni	-	Middle Triassic
Notobrachyops picketti	-	? Upper Triassic

The diagnostic characters of the family have been honed down to the following: short, broad skull; large usually anterior orbits; absence of otic notch; lack of tabular horns; very large palatal tusks; strongly sloping occiput; deep cheek region, highly vaulted palate; pronounced squamosal-quadratojugal trough on occiput lateral to pterygoid, the latter expanded posteriorly.

TABLE I WORLD DISTRIBUTION OF BRACHYOPIDAE

	U.S.A.	SPITZBERGEN AND U.S.S.R.	INDIA	AFRICA	AUSTRALIA	ANTARCTIC
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 Anisian (Kitching in press)

2. THE FAMILY CAPITOSAURIDAE

Class Amphibia

Subclass Labyrinthodontia

Order Temnospondyli

Family Capitosauridae

2.1 *Parotosaurus africanus* (Broom 1909) Synonym: *Capitosaurus africanus* Broom 1909 (Ann. S. Afr. Mus., 7, 270-273)

Type: Fragmentary skull and part of left lower jaw, S.A.M. Cat. No. 2360

Locality: Vaalbank, Albert, C.P.

Horizon: *Cynognathus* zone

Hypodigm: S.A.M. Cat.No.3008 from Winnaarsbaken,Albert,C.P. (complete skull except for dorsal surface - this skull could not be traced)

2.1.1 Diagnosis

A *Parotosaurus* with a skull of average breadth (B:L approximately ?70) and shallow posteriorly (H:B approximately 17); orbits close together (A:L approximately 16), separated by a shallow depression, well posterior, oval with long axes converging anteriorly; large circular pineal foramen, close to hind border of orbits (P:C ≈ 14); otic notches semiclosed with tabular horns distinctive, expanded distally towards squamosal; supratemporal excluded from otic notch; postorbital not in contact with parietal; posterior skull border concave K:C = 28); exoccipitals well exposed on palate; pterygoid bears fine sculpturing.

2.1.2 Description of the material

The bones of the skull (figs. 1, 2, 3, 4) Unless otherwise stated, the left side of the skull is described because it is the best preserved.

The parietal: Anteriorly, the suture between the frontal and the parietal is almost straight transverse to the midline. Laterally, the suture with the postfrontal is first straight and parallel to the midline, so that the anterolateral corner of the parietal forms almost a right angle. Then, the anterolateral parietal-postfrontal suture slants towards the otic notch. The parietal meets the supratemporal posterolaterally in a sinuous suture concave to the midline. Posteriorly, the parietal abuts the postparietal in an almost straight suture transversely to the midline. A circular parietal foramen is situated on the midline almost in the centre of the two parietals.

The postparietal: The postparietal sutures anteriorly with the parietal as previously noted. Anterolaterally, the postparietal sutures with the supratemporal in a posterolaterally slanted suture, while posterolaterally,

the suture with the tabular slants oppositely in a posteromedial direction. The postparietal forms the centre limit of the skull. When viewed dorsally, this posterior border is curved. The postparietal also forms the upper median border of the occiput. The posterior edge of the skull roof is thickened. The ventral process which meets the postparietal process of the exoccipital is not preserved on the right side.

The postfrontal: The anterior limit of the postfrontal is missing. Anterolaterally, the postfrontal forms the posteromedial border of the orbit. Posterolaterally, the postfrontal sutures with the postorbital in a posteromedially slanted suture. Anteromedially, a small part of the postfrontal-frontal suture is preserved which is almost straight and parallel to the midline. Posteromedially, the suture with the parietal is first straight and parallel to the midline and then slants obliquely towards the otic notch. Posterolaterally, the postfrontal has a short suture with the supratemporal.

The supratemporal: The supratemporal has a roughly pentagonal shape. Anteriorly, it sutures with the postorbital and postfrontal in an irregular suture almost transverse to the midline. Laterally, the supratemporal meets the squamosal in a slightly posteromedially slanted suture. Anteromedially, the suture with the parietal is irregular and concave to the midline. Posteromedially, this suture is continued in a posterolateral direction. Posteriorly, the supratemporal joins with the tabular in an almost straight suture transverse to the midline. It is almost excluded from meeting the postfrontal by contact between postorbital and parietal, but just touches the postfrontal anterolaterally, thus preventing the meeting of the parietal and postorbital.

The tabular: Anteriorly, the tabular meets a small part of the squamosal laterally and then continues medially with the supratemporal in a more or less straight suture transverse to the midline. Medially, the tabular meets the postparietal in a posteromedially slanted suture. The tabular forms a rounded posterolateral projection which is the tabular horn. This forms the posteromedial border of the otic notch. The distal portion of the tabular horn is slightly expanded anteriorly and laterally, thus constricting the posterior opening of the otic notch, behind the tympanic area. The tabular also forms the upper border of the occiput lateral to the postparietal.

It forms a process ventromedially which probably met the exoccipital

but which is disarticulated in the specimen. This region of the skull is slightly distorted due to dorso-ventral flattening.

The postorbital: Anteriorly, the postorbital forms the posterior border of the orbit. The anterolateral limit of the postorbital is not preserved. Posterolaterally, the postorbital meets the squamosal in a sinuous posteromedially slanted suture. It meets the supratemporal posteriorly in an irregular suture almost transverse to the midline.

The squamosal: The anterior limits of the squamosal are not preserved. Anteromedially, the squamosal meets the postorbital in a sinuous posteromedially directed suture, then continues to suture with the supratemporal in an almost straight slightly posteromedially slanted suture. The posteromedial corner of the squamosal has a short straight suture with the tabular. Posterolaterally the squamosal meets the quadratojugal in a straight suture almost parallel to the midline which lies in the depression of the jugal lateral-line canal. Laterally, a small curved section of the suture with the jugal is preserved. Posteriorly, the squamosal forms the anterolateral border of the otic notch. In occipital view, the squamosal has a descending flange which forms the dorsal portion of the anterior wall of the stapedial groove. This flange meets the ascending ramus of the pterygoid. Laterally to this flange, the squamosal forms the entire occipital wall above the quadrate and medial to the quadratojugal.

The quadratojugal: The quadratojugal forms the posterolateral limit of the skull table. Medially, it sutures with the squamosal in a straight suture parallel to the midline. This suture lies in the depression of a lateral-line canal. Anteriorly, the quadratojugal meets the jugal in an almost straight suture transverse to the midline. The quadratojugal forms the posterolateral corner of the palatal surface and in occipital view it forms the extreme lateral part of the posterior wall of the skull. It is perforated by the paraquadrate foramen. In occipital view the quadratojugal sutures medially with the quadrate and is dorsally overlapped by the squamosal.

The jugal and maxilla: Small fragments of the jugals and the maxillae are preserved.

The Sculpture

The sculpture is of the type found throughout the Capitosauroidea. In the centre of each bone are small irregular pits from which, in the larger bones ridges and grooves radiate outwards.

The Lateral Line System

The supraorbital canal is partially preserved, following the curve along the posteromedial border of the orbit, as a series of enlarged pits surrounded by broader than average ridges.

The jugal canal is partially preserved as a deep groove running along the quadratojugal-squamosal suture.

The temporal canal is not evident, probably due to the large number of cracks in the supratemporal region.

The Orbits

Only the posteromedial borders of the orbits are preserved, but the impression of both orbits is quite clear on the matrix. They are oval with their long axes oblique to the midline, converging anteriorly. The orbits measure approximately 3cms by 2cms.

The Palate

The parasphenoid: The parasphenoid consists of a posterior basal plate which has been severely distorted and a small posterior portion of the narrow cultriform process. The ventral surface of the cultriform process is badly cracked. The basal plate of the parasphenoid is concave in cross section. It meets the pterygoids laterally in interdigitated oblique sutures. The basal plate has a short free edge between the exoccipital condyles. The crista muscularis is preserved as a ridge of bone. Posterior to this ridge, the medial part of the parasphenoid is deflected towards the skull roof. This distortion is probably due to post-mortem damage.

The pterygoid: The pterygoid consists of a body with a palatine ramus and a quadrate ramus. The body meets the basal plate of the parasphenoid in an interdigitated oblique suture which runs posterolaterally from the centre of the posterior border of the interpterygoid vacuity to the posterior edge of the palate. This region, as noted previously, has been distorted, but as it is preserved, the pterygoid does not seem to meet the exoccipital in palatal view. Fine sculpturing is present on the lateral surface of the body where it borders the subtemporal fossa, and on the lateral part of the palatine ramus. The medial side of the palatine ramus is curved and is not sculptured. Anteriorly the limits of the palatine ramus are missing. The quadrate ramus bears no sculpturing. It ends on the left side of the skull in a sinuous suture with the quadrate. In occipital view the dorsal surface of the quadrate ramus

is extended into an ascending ramus which meets the descending flange of the squamosal. The pterygoids, seen posteriorly, cover different areas on the left and right of the skull, which is probably due to distortion.

The interpterygoid vacuities: These converge posteriorly to a broad point. The anterior borders are missing.

The ectopterygoid: Lateral and anterior to the palatine rami of the pterygoids displaced ectopterygoids carrying tooth bases are present.

The quadrate: The quadrate forms the articular surface for the lower jaw. Anteriorly, in palatal view, it forms the posterior border of the subtemporal vacuity. Its medial suture with the quadrate ramus of the pterygoid is sinuous and posteromedially slanted. Laterally, the quadratojugal clasps the quadrate with anterior and posterior flanges which surround the lateral extremity of the bone. This lateral part of the quadrate is a rounded condyle. Anteromedially, a larger condyle is present with a groove just posterior to it. Behind this groove the posteromedial corner of the quadrate forms a distinct angle of smooth-surfaced bone which perhaps assisted as an auxiliary articulatory area. Between the lateral and anteromedial condyles is the trochlear which lies parallel to the medial condyle.

In occipital view, the quadrate forms about a quarter of the wall of the back of the skull. Dorsally, it meets the squamosal in a wavy, ventrolaterally directed suture. Medially, it meets the quadrate ramus of the pterygoid in an irregular suture almost perpendicular to the skull. Laterally, the quadratojugal meets the quadrate with a dorsal and ventral flange which surrounds the lateral margin of that bone.

The Occiput

The exoccipital: The left exoccipital, which is better preserved, is subcircular. It faces inward and downward and has a roughened surface that evidently bore a cap of cartilage. In palatal view the exoccipital extends forwards to meet the basisphenoid and not the pterygoid. However, this area is distorted as discussed earlier. In occipital view, the exoccipital sends up a stout process that bifurcates to form the vertical postparietal process and the dorsolateral tabular process. The left exoccipital is different from the right and seems less distorted. The vertical postparietal process has two medial extensions. The upper one, the processus lamellosus, evidently underlay a cartilaginous supraoccipital. It

resembles a vertebral prezygopophysis. It is noted here that the left exoccipital seems to have two vertical dorsal postparietal processes with a distinct groove between them. This may be due to distortion, but the two pillars are smooth and intact. The lower medial process of the postparietal process, the processus basalis, approaches the midline and overlies the space presumably occupied by the cartilaginous basioccipital. On the lateral wall of the exoccipital, just above the condyle, lies the posterior opening for the XIIth nerve. Its internal opening is on the anteromedial face of the dorsal process just above the processus basalis. Laterally and ventral to the posterior opening for the XIIth nerve lies the smaller foramen, presumably for the Xth nerve, which is not seen in the illustrations. The tabular process of the exoccipital projects dorsolaterally and somewhat posteriorly to meet the tabular. This area on both sides of the skull is badly distorted. Between the postparietal and tabular processes of the exoccipital lies the triangular posttemporal fenestra.

The Lower Jaw

About 22cms of the left lower jaw is preserved. The piece tapers from 5cms posteriorly to 1.5cms anteriorly. Lingually, an anterior Meckelian foramen is present on what is presumably the postsplenial. Although the two bones are disarticulated, it is clear that lingually the postsplenial met the splenial in an almost straight ventromedially slanted suture. Above the postsplenial lies the intercoronoid. Its sutures with the postsplenial ventrally and the dentary dorsally are not discernible. Between the splenial dorsally and the dentary ventrally lies the precoronoid which forms a thin ribbon of bone. Its posterior suture with the intercoronoid is not discernible, and anteriorly its limits are not preserved.

Labially, the dentary, which dorsally bears a single row of uniform tooth-bases, forms most of the jaw fragment. Posteroventrally, lies the anterior part of the angular which is sculptured. The angular meets the unsculptured dentary dorsally in an irregular, anteroventrally directed suture. The posterior limits of the angular are not preserved. Anteriorly, the angular meets the postsplenial in an irregular posteroventrally oblique suture. The postsplenial meets the dentary dorsally in an almost straight suture parallel with the ventral surface of the jaw fragment. Anteriorly, the postsplenial meets the splenial in an irregular suture which dorsally slants posteroventrally, but ventrally is not discernible. Dorsally, the splenial meets the dentary in an almost straight suture parallel to the

ventral edge of the jaw fragment. The labial side of the splenial and post-splenial is sculptured in radial high and sharp ridges and broad, flat grooves

2.1.3 Discussion

Welles and Cosgriff (1965) stated that 'Capitosaurus africanus' was never figured and the description was not adequate for generic or specific determination. The species was therefore designated nomen vanum. As shown, however, the specimen consists of most of the postorbital parts of the skull which are fairly well preserved and may be directly compared with the same parts on other taxa.

Howie (1970) states that 5 species of parotosaurs have a tabular horn which has grown laterally towards the squamosal. These are P. semiclausus (Swinton 1927), P. birdi (Brown 1933), P. peabodyi Welles and Cosgriff 1965, and P. brookvalensis Watson 1958. In P. pronus, Howie 1970, the tabular horn is expanded anteriorly and laterally towards the squamosal so that the otic notch is semiclosed. This distal expansion of the tabular horn occurs also in P. rajareddyi Chowdhury 1970, P. megarhinus Chernin and Cosgriff 1975, and also P. africanus (Broom 1909). (Figs. 1a, 3)

In Table II a comparison is made between P. pronus, P. africanus and P. megarhinus. The measurements for P. africanus are derived from the reconstruction to overcome the limitations of distortion during fossilization. From the range of indices shown in this Table, it is probable that these three parotosaurs are closely related. P. africanus probably had a narrower skull than the other two forms. (It is noted here that the skull length is only an estimated figure). The interorbital breadth is probably greater than that of both the other forms. The interotic breadth is greater than P. megarhinus but the same as that of P. pronus. The interorbital length to interotic length index is slightly greater than both P. pronus and P. megarhinus which have the same index value. The distance between the orbit and the otic notch is greater than that of the other two forms in which this value is approximately the same. The distance behind the orbits of the parietal foramen is also greater than that of the other two forms for which this value is also more or less the same. The distance between the parietal foramen and the front of the otic notch is greater than that of the other two forms. The concavity of the posterior border of the skull is less than in P. pronus, but greater than that of P. megarhinus.

Thus in three out of eight indices, P. africanus is closer to

P. pronus (i.e. A:L, C:L and K:C); in two indices P. africanus is closer to P. megarhinus (i.e. B:L and N:C). In two indices it is equally apart from both (T:C and P:C) and finally in one index it has approximately the same value (A:C).

Thus it would seem that these three pa otosaurs are on very much the same evolutionary level. P. pronus is thought to be Mid-Triassic, P. megarhinus to be on the border of the Lower-Middle Triassic, and P. africanus is from the Cynognathus zone. Thus, on the basis of the comparative morphology of these three species, the Cynognathus zone would seem to be close to the Lower-Middle Triassic boundary.

TABLE II- Measurements of reconstructed skull of Parotosaurus africanus

Indices (from Welles and Cosgriff, 1965)		Cms.
Height of postparietals above parasphenoid	H	3.4
Breadth of skull across quadrates	B	20.0
Estimated length of skull	L	28.5*
Interorbital distance taken at midlength of orbit	A	4.6
Estimated distance from tip of snout to level of anterior edge of orbit	O	19.0*
Distance from level of posterior limit of orbit to level of centre limit of skull	D	6.5
Distance from posterolateral corner of eye to otic notch	N	5.7
Midline distance from centre posterior limit of skull to level of posterior limit of tabular horn	K	2.8
Distance between otic notches	C	10.0
Distance from mid-length of orbit to lateral edge of same side	I	4.6
Distance from level of posterior limit of orbit to parietal foramen taken at centre of skull	P	1.4
Mid-line distance from level of anterior limit of otic notch to parietal foramen	T	3.4

* From reconstruction

Author Chernin S
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