SOUTHERN AFRICAN TRIASSIC LABYRINTHODONTS: THE CAPITOSAURIDAE AND THE BRACHYOPIDAE

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This thesis is submitted in the
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ABSTRACT

Two members of the Family Capitosauridae are redescribed after further
preparation, namely *Parotosaurus africanus* (Broom 1909) and *Kestrosaurus*
dreyeri Haughton, 1925. New material consisting of a fragmentary lower
jaw of a very large parotosaur from the *Cynognathus* zone of Aliwal North
is described, upon which a new species *Parotosaurus dirus* is erected.

Parotosaurus africanus (Broom 1909) from the *Cynognathus* zone of
Vaalbank, Albert, Cape Province, is redescribed and figured for the first
time. It consists of most of the postorbital regions of the skull
associated with part of the left lower jaw which are fairly well preserved
and capable of being directly compared with the same parts on other taxa.
Thus it is reconfirmed a valid member of the family Capitosauridae.

Kestrosaurus dreyeri is re-examined and found to consist of large areas
of Plaster of Paris in which the original bone has been embedded. The entire
skull could be about 5 cm shorter than the original reconstruction. The
position and shape of the orbits are not preserved and the reconstructed
lateral position found in the specimen is arbitrary. The parietal foramen
is also not preserved. The nature of the preserved palate and occipital area
indicates that the material probably represents a primitive member of the
family Capitosauridae, not only stratigraphically (*Lystrosaurus* zone), but
also morphologically. The taxonomic designation established by Welles and
Cosgriff (1965) is retained. *Kestrosaurus* remains an enigma because it also
displays certain trematosaurid characters.

A partial capitosaurid jaw from the *Cynognathus* zone of Aliwal North,
Cape Province, is also described which when reconstructed represents one of
the largest amphibians found in Southern Africa. Comparisons are made with
Parotosaurus pronus Howie, 1970 and *Parotosaurus megarhinus* Chernin and
Cosgriff 1975, which share a few similar characteristics. It is suggested
that the amphibian represented by this jaw may be ancestral to both *P. pronus*
and *P. megarhinus*. Based on substantial morphological differences in the
symphysial and articular regions between this jaw and those of the above
mentioned parotosaurs, it is hereby proposed to erect a new species,
Parotosaurus dirus (dirus = Latin: fearful) for this material.

A world-wide survey of the Family Brachyopidae is undertaken.

Batrachosuchus concordi (sp.nov.) from the N'tawere Formation in the Upper Luangwa Valley, Zambia is described. In general shape, B. concordi mostly resembles Batrachosuchus watsoni, except for size where the former is much smaller. Stratigraphically, it seems that B. concordi is more or less on the same level as the Cynognathus zone batrachosuchians.

Batrachosuchus browni, Broom 1903 is described after further preparation. Four specific differences are observed which separate B. browni from the other Cynognathus zone batrachosuchian, Batrachosuchus watsoni. These are: the presence in B. browni of (1) an interfrontal (2) a vomerine foramen (3) the paraspheniod does not reach the edge of the palate as it does in B. watsoni and (4) the wider lateral line canals of B. watsoni and their distribution.

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

tr — trough for depressor mandibular muscle

v   — vomer

ven — ventral process

vf — vomerine foramen

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1. INTRODUCTION

1.1 The family Capitosauridae

The capitosaurs were among the earliest fossil amphibians to be discovered. Mastodonsaurus 'giganteus' (Jaeger, 1828) from the Lettenkohle of Gaildorf in Germany was the first labyrinthodont to be described (Paton, 1974). Since then, many new genera and species have been discovered and named. Watson (1962) discussed various evolutionary trends in the morphology of the group e.g. progressive closure of the otic notch; progressive chondrification (especially noticeable in the neurocranium and limb bones); increase in dorsoventral flattening of the skull; and an increase in size.

Welles and Cosgriff (1965) revised the group, relegating a large number of generic and specific names to the nomen vanum category and reducing the taxonomic content to 3 families, 6 genera and 18 species. The families retained by them within the superfamily Capitosauroidea are the Bentho- suchidae, Mastodonsauridae and Capitosauridae. Within the Capitosauridae Parotosaurus has 8 species: P. nasutus (Meyer) 1858; P. helgolandicus (Schroeder) 1913; P. haughtoni (Broili and Schroeder) 1937; P. semiclausus (Swinton) 1927; P. angustifrons (Riabinin) 1930; P. brookvalensis (Watson) 1958; P. birdi (Brown) 1933 and P. peabodyi Welles and Cosgriff, 1965. Cyclotosaurus has 4 species: C. robustus (Quenstedt) 1850; C. stantonensis (Woodward) 1904; C. ebrachensis Kuhn 1932 and C. hemprichi Kuhn, 1942. Kestrosaurus has 1 species K. dreyeri Haughton 1925 and Paracyclotosaurus has 1 species P. davidi Watson, 1958.

Since the time of the Welles and Cosgriff revision, the contents of the family have been enlarged and many changes in its structure have been proposed. Otchev (1966) was responsible for   of this, but his work is not generally available. These alterations and additions although adding greatly to the knowledge of the morphology, diversity and geographic distri- bution of the group, have left capitosaurid taxonomy in a confused and unreconciled state. A complete new revision of the superfamily Capitosauroi- dea is therefore called for, but this is beyond the scope of the present investigation (see Chernin and Cosgriff 1975).

Thus the aim of this investigation is to reconsider only the Karroo Capito- sauridae. The forms dealt with here are as follows:

Parotosaurus africanus (Broom) 1909 was considered nomen vanum by Welles and Cosgriff (1965) as they believed the holotype of this form was too incomplete for meaningful comparisons. The specimen, however, consists of most of the postorbital portions of the skull which are well prepared and capable of being compared directly with these portions in other taxa.

Kestrosaurus dreyeri Haughton, 1925 is obviously close to other parotosaurs but remains enigmatic because of some trematosaur characters which it possesses.

A very large fragmentary capitosaur jaw from Aliwal North, Cape Province is described as a new species, Parotosaurus dirus.

Clearly, however, the uncertainty in the classification of the group must affect this effort (Chernin and Cosgriff, 1975).

Welles and Cosgriff (1965) overlooked the following taxa that were described in the years just previous to the publication of their review: Cyclotosaurus mechernichensis Jux and Pflug (1958) from the Muschelkalk of of West Germany; Promastodonsaurus bellmani Bonaparte (1963) from the Ischigualasto Formation of Argentina; and Parotosaurus orenburgensis Konzhukova, (1965) from zone VI of the Cis-Uralian sequence of the Soviet Union. All three of these were placed in the family Capitosauridae by the authors.

Further new genera and species have been added to the superfamily since the revisions of Welles and Cosgriff (1965). These are, by stratigraphic unit and region: from the Triassic portion of the Cis-Uralian region of the U.S.S.R. - Benthosuchus bashkirikus Otchev (1973); from the Lower Triassic of Sinkiang - Parotosaurus turfanensis Young (1965); from the Upper bunter of West Germany - Eocyclotosaurus woschmidti Ortlam (1970); from the Lower Triassic of the Vosges, France - Stenotosaurus lehmani Heyler (1969); from the Lower Triassic Zarzaitine Series of Algeria - Parotosaurus lapparenti Lehman (1971) and Wellesaurus bussoni Lehman (1971); from the Yerrapalli Formation of India - Parotosaurus rajareddyi Chowdhury (1970); from the Middle Triassic Manda Formation of Tanzania - Parotosaurus pronus Howie (1970); from the Lower Triassic Gosford Formation of New South Wales - Parotosaurus wadei Cosgriff (1972); from the N'tawere Formation in the Upper Luangwa Valley, Zambia - Parotosaurus megarhinus Chernin and Cosgriff (1975).

Further alteration in generic assignments and familial groupings have also appeared in recent literature: Jux (1962) changed Cyclotosaurus mechernichensis to Procyclotosaurus mechernichensis and later (Jux 1966)

to Parotosaurus mechernichensis. Heyler (1969) removed Stenotosaurus from
the Capitosauridae, placing it in its own family Stenotosauridae. Lehman
(1971) changed Parotosaurus peabodyi to Wellesaurus peabo i. Paton (1974)
revalidated the 3 species Labyrinthodon leptognathus, Owen, 1842,
Labyrinthodon pachygnathus Owen (1842) and Labyrinthodon lavisi Seeley (1876),
placing the first two in Cyclotosaurus and the last in Mastodonsaurus. Paton
placed Cyclotosaurus stantonensis (Woodward, 1904) as referred specimen of
C. leptognathus and supported Heyler's segregation of Stenotosaurus in its
own family Stenotosauridae, adding to this family Kestrosaurus dreyeri
Haughton (1925).

Otchev (1966) contributed an extensive consideration and revision of
capitosaurid systematics and phylogeny, summarised in Chernin and Cosgriff
(1975). A discussion of his treatment of the Superfamily at species level
is omitted here as none of this is presently relevant to a reconsideration
of the Karroo amphibians. The classification of the Capitosauroidea of
Otchev (1966) down to generic level is as follows:

Superfamily Capitosauroidea

    Family Rhinesuchidae Watson, 1919

        Rhinesuchus Broom, 1908

        Rhinesuchoides Broom and Olson, 1937

        ? Jugosaurus Riabinin, 1962

    Family Uranocentrodontidae Romer, 1947

        Uranocentrodon Hoepen, 1917

        Laccocephalus Watson, 1919

        ? Muchocephalus Watson, 1962

        ? Gondwanasaurus Lydekker, 1885

        ? Pachygonia Huxley, 1865

    Family Rhinecepidae Otchev, 1965

        Rhineceps Watson, 1962

    Family Lydekkerinidae Watson, 1919

        Lydekkerina Broom, 1915

    Family Sclerothoracidae Huene, 1931

        Sclerothorax Huene, 1931

    Family Capitosauridae Watson, 1919

        Subfamily Wetlugasaurinae Otchev, 1958

            Wetlugasaurus Riabinin, 1930

        Sassenisaurus Nilsson, 1942

        Parotosaurus Jaekel, 1922

        Karoosuchus Otchev, 1966

        Watsonisuchus Otchev, 1966

        Stenotosaurus Romer, 1947

        Eryosuchus Otchev, 1966

        Mentosaurus Roepke, 1930

        Capitosaurus Münster, 1836

    Subfamily Cyclotosaurinae Otchev, 1966

        Procyclotosaurus Watson, 1958

        Cyclotosaurus Fraas, 1889

    Subfamily Paracyclotosaurinae Otchev, 1966

        Subcyclotosaurus Watson, 1958

        Paracyclotosaurus Watson, 1958

        Austropelor Longman, 1941

        Stanocephalosaurus Brown, 1933

        Moenkopisaurus Shishkin, 1960

        Rhadalognathus Welles, 1947

  Family Mastodonsauridae Lydekker, 1885

        Heptasaurus Säve-Söderbergh, 1935

        Mastodonsaurus Jaeger, 1828

        Promastodonsaurus Bonaparte, 1963

  Family Bukobajidae Otchev, 1966

        Bukobaja Otchev, 1966

        Kestrosaurus Haughton, 1925

        Meyerosuchus Otchev, 1966

  Family Benthosuchidae Efremov, 1931

        Benthosuchus Efremov, 1929

        Yarengia Shishkin, 1960

In comparing this classification with that of Welles and Cosgriff (1965) many differences will be noted (see page 1 above). Among these are the much greater number of previously described genera recognised by Otchev, the addition of new genera and families, the inclusion of the families Rhinesuchidae, Uranocentrodontidae, Lydekkerinidae and Sclerothoracidae in the superfamily and the division of the Capitosauridae into subfamilies.

    Reliable comparisons are limited in this chapter to those species for which extensive sets of measurements of the skull roof are available. These

include the species recognised by Welles and Cosgriff (1965): Parotosaurus
nasutus, P. helgolandicus, P. haughtoni, P. semiclausus, P. angustifrons,
P. brookvalensis, P. birdi, P. peabodyi and Paracyclotosaurus davidi.
Comparisons of this nature are also possible with Parotosaurus mechernichensis
P. pronus, P. rajareddyi, Wellesaurus bussoni, P. wadei, P. lapparenti,
P. orenburgensis and P. megarhinus.

1.2 The family Brachyopidae

The brachyopid labyrinthodonts were carnivorous amphibians which existed
from the Upper Permian to the Upper Triassic. Some were as large as 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 family as to its contents and taxonomic
history.

Watson (1919), defined the family Brachyopidae as follows: Temnospon-
dyls having:

1. Broad parabolic skulls with large, anteriorly situated orbits.
2. A flange of the squamosal which wraps around the outer side of the
    quadrate, and having thus formed a concave face on the occipital
    surface, ends in a ridge, separated by the quadrate from an exactly
    similar ridge of the pterygoid.
3. A down-turning of the lateral wings of the pterygoid from the
    subtemporal fossae, so that the palate forms a broad ∩-shaped arch.
4. Occipital condyles which lie far behind the parietals so that the
    occipital surface slopes forward.

Watson (1926) suggested that Dvinosaurus was a possible ancestor of
the brachyopids, pointing out the existence of branchial arches and
suggesting that the animal was neotenous. Sushkin (1936) described the
animal and accepted the view that Dvinosaurus and Batrachosuchus are close
relatives, though noting that as Dvinosaurus is neotenous it cannot be an
actual ancestor of the other form. He also noted the remarkable similarity
between the stapes of the two animals - a matter of importance, for the
massive bone differs greatly from those of all other labyrinthodonts.
Bystrow (1939) agreed that in general appearance the skull of Dvinosaurus
resembles the brachyopids, but found a series of differences. However,
most of these differences were the results of parallel evolutionary change
of the characteristically labyrinthodont type.

Watson (1956) included the plagiosaurs in his survey of the brachyopid line, because he thought that close relationship between the Upper Permian and Lower Triassic typical brachyopids and the Middle and Upper Triassic plagiosaurs obvious, because of special common peculiarities not apparently known in any other contemporary labyrinthodonts. However, Panchen (1959) showed that the plagiosaurs were not closely allied to the brachyopids, because their similarities in skull form could be attributed to functional adaptation. Many of the adaptations, though producing analogous skull features, are probably aimed towards different modes of life in the two groups so that the similarities are superficial.

Watson (1956) reached the conclusion that the following species are members of a group of labyrinthodonts relatively closely allied to each other though not members of a single lineage:

Bothriceps australis, ? Mid-Permian

Eobrachyops townendae, Clear Fork, U-Permian

Eobrachyops casei, Clear Fork, U-Permian

Dvinosaurus primus, U-Permian

Trucheosaurus major, U-Permian

Brachyops laticeps, Permo-Triassic boundary

Batrachosuchus browni, L-Trias

Batrachosuchus watsoni, L-Trias

'Platyceps' wilkinsoni, L-Trias

Plagiosternum granulosum, M-Trias

Plagiosuchus pustuliferus, M-Trias

Gerrothorax rhaeticus, U-Trias and Rhaetic

Plagiosaurus depressus, ? Rhaetic

It was thus possible to recognise changes in structure that persist over all or some part of the long life of the family, viz:

1. The large, single, mainly basioccipital condyle of Eobrachyops evolves into the wide tripartite condyle of Dvinosaurus, and that changes to the condition where the exoccipital condyles are separated and the basioccipital is absent as in Batrachosuchus.

2. The ossified supraoccipital of Eobrachyops and Dvinosaurus vanishes in the later forms.

3. The extensive exoccipital of Eobrachyops, although reaching the tabular, does not extend forward to the pterygoid as it does to an increasing extent in Bothriceps, Batrachosuchus and the 'plagiosaurs'.

4. The pterygoid, movably articulated with the parasphenoid in _Eobrachyops_ and _Dvinosaurus_, gains a sutural attachment to the lateral border of the parasphenoid in _Bothriceps_, which steadily increases in extent in subsequent genera, by backward spreading of the exoccipital.

5. The hypoglossal foramen perforates the exoccipital of _Eobrachyops_, but lies on the lateral surface of that bone in _Bothriceps_; it emerges through the hinder surface in _Batrachosuchus_ and it is not seen in _Gerrothorax_.

6. The occipital aspect of the skull of _Eobrachyops_ shows a deep occiput and ventrally placed quadrate condyles. _Bothriceps_, _Batrachosuchus_ and _Gerrothorax_ show a progressive flattening, both of the lateral suspensory part of the skull and of the occiput.

7. The quadrate, which in _Eobrachyops_ is on the level of the occipital condyle when the skull is viewed laterally, moves forward in late forms such as _Batrachosuchus_ and _Gerrothorax_.

8. The retroarticular process of the lower jaw, present in _Eobrachyops_, enlarged in _Bothriceps_, becomes still longer in _Batrachosuchus_ and immense in _Plagiosuchus_.

9. The intertemporal, present as an independent bone in _Eobrachyops_, fuses with the postorbital in _Dvinosaurus_ and vanishes in _Batrachosuchus_ and all later forms, bringing the supratemporal into contact with the postfrontal.

10. _Eobrachyops_ has protorhachitomous vertebrae. In _Dvinosaurus_ they are rhachitomous, though the first vertebra lacks a pleurocentrum and those of the next two fuse with the intercentra and neural arches. In plagiosaurs the neural arch and intercentrum alone remain, the latter bone taking on the appearance of a centrum.

Thus, in all important matters, the course of evolutionary change in brachyopids is uniform in direction over the immensely long history of the group and is parallel in some respects to that found in the Capitosauridae.

Cosgriff (1969) states that the superfamily Brachyopoidea contains only the families Brachyopidae and Dvinosauridae. The family Dvinosauridae was originally proposed by Säve-Söderbergh (1935) but he suggested a separate superfamily, the Dvinosauroidea. Cosgriff (1969) diagnosed the superfamily Brachyopoidea as follows: "skull broad and parabolic. Orbits in anterior part of skull roof. Otic notch absent or rudimentary. Orbital and

antorbital regions of the skull relatively shallow. Cheek deep. Palate highly vaulted in occipital aspect. Occipital portions of the squamosal and quadratojugal concave in posterior view. Long narrow fissure between the squamosal and pterygoid. In addition, the following feature of the lower jaw construction is uniform through all species of the superfamily for which the lower jaw is known: posterior meckelian foramen and angular-prearticular suture on ventral surface or very low on lingual surface".

The family Dvinosauridae is diagnosed by Cosgriff (1969) as follows: "occipital condyles directly beneath and posterior to edge of the skull roof. Basicranial joints present between the basisphenoid and pterygoid bones, pterygoid bones not joined by suture to parasphenoid bone. Palatal tooth row present on ectopterygoid and palatine bones as well as on vomer".

The family Brachyopidae is diagnosed by Cosgriff, 1969 as follows: "occipital condyles far behind the posterior edge of the skull roof. Basicranial joints absent; pterygoid bones joined by suture to parasphenoid bones. Palatal teeth present only on vomer".

Cosgriff (1969) reviews the evolution of the family Brachyopidae stating that the three trends cited by Watson (1919) in structural modification of the brachyopid skull in successive stages marked by the Late Permian genera Dvinosaurus and Bothriceps, the early Triassic Batrachosuchus and the late Triassic Plagiosaurus, still apply to the other genera although Plagiosaurus and its allies are now removed to a separate order (Panchen, 1959) or suborder (Romer, 1966). These trends are:

1. A progressive movement forward of the quadrate condyles from a position level with the hinge line of the exoccipital condyles to an anterior position.

2. The exoccipital and pterygoid bones do not meet in Dvinosaurus. There is a short suture between these elements in Bothriceps and a wide suture in Batrachosuchus.

3. In Bothriceps, the hypoglossal foramen is on the lateral surface of the exoccipital. In Batrachosuchus it is on the posterior surface of the bone, directly above the condyle.

Welles and Estes (1969) redefined the Brachyopidae as follows: skull short and broad; B:L index from 110 to 150; no zones of relative intensive growth. Orbits anterior and usually relatively large. Otic notch absent or at most a shallow embayment. Tabulars short and broad; tabular horns absent or weak.

Parasphenoid flat, becoming elevated anteriorly above vomers. Usually a tusk-pit pair on vomer, palatine and ectopterygoid; interstitial smaller teeth little developed or absent; tusks usually much elongated and massive; dentary tooth row relatively short. Vomerine plate short. Occiput with strong slope posteroventrally to occipital condyles, the latter usually quite large. Quadrate condyles large, ventrally produced , anteroventral in position relative to occipital condyles. Squamosal and quadratojugal with strong occipital flange forming a vertical, transversely concave trough lateral to the pterygoid. Retroarticular process elongate. Pterygoid forming large vertical plate laterally that is posteriorly elongated beyond squamosal quadratojugal trough, forming a steeply arched, flat-roored palate. Quadrate somewhat compressed laterally, wedged anterolaterally between flange of pterygoid and squamosal - quadratojugal trough.

Using the three diagnoses already quoted, a composite diagnosis of the family Brachyopidae may be set down as follows: skull short and broad: B:L index 110 to 150; no zones of relative intensive growth; occipital condyles far behind posterior edge of skull roof; basicranial joints absent; pterygoid bones joined by suture to parasphenoid bones; palatal teeth present only on vomer; squamosal and quadratojugal with strong occipital flanges forming a vertical, transversely concave trough lateral to the pterygoid; pterygoid forming a large vertical plate laterally that is posteriorly elongate beyond squamosal-quadratojugal trough, making a steeply arched flat-roofed palate.

Workers have at various times removed genera from the Brachyopidae. Panchen (1959) - as already mentioned - 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 ?) series near Tungus, Siberia. It may be of Early Permian age (Olsen, 1962). It was removed due to the controversy surrounding the centra: if the centra of *Tungussogyrinus* are solid and elongate as described by Efremov (1939), they are not indicative of brachyopid affinity. However, the illustration by Bystrow (1939) shows short broad intercentra that would be brachyopid.

Thus better specimens are needed before the relationship of this form can be determined.

Boreosaurus thorslundi Nilsson, 1943, from the Early Triassic of Spits-bergen. The very short retroarticular process excludes this form from the Brachyopidae - this structure is even shorter than that of the primitive Dvinosaurus.

Pelorocephalus mendozensis Cabrera, 1944 from Potrerillos Village, Mendoza Province, Argentina, in the Upper Cacheuta beds of Early or Middle Triassic age. Following Cabrera's (1944) description of P. mendozensis, Rusconi made known a remarkable series of closely related specimens that he named Chigutisaurus tunuyanensis (1948), C. tenax and C. cacheutensis (1955). The relationship and taxonomy of the labyrinthodonts are not yet settled, but Welles and Estes (1969) agree with Reig (1961) that only one genus is represented. They bear little resemblance to brachyopids, and lack all characters that Welles and Estes (op. cit.) believe to be diagnostic of the group. A table of indices prepared by Welles and Estes (op. cit.) reveals their close relationship to each other and their distinctiveness from the brachyopids.

Tupilakosaurus heilmani Nielsen, 1954 is from the Early Triassic of Greenland. Nielsen (1967) reinterpreted the type specimen of this species and states that Tupilakosaurus resembles the brachyopids and that its embolomerous centra probably indicate the nature of the brachyopid vertebral column. Shishkin (1961) has described a more complete skull roof and referred it to a different species Tupilakosaurus wetlugensis from Early Triassic deposits of the Vetluga basin. This skull lacks the strong pro-trusion of the occiput and the posterior widening, possesses a lacrimal bone and minute tabulars. No brachyopid has a lacrimal, nor is the tabular reduced as much in any brachyopid as it is in Tupilakosaurus. The para-sphenoid and pterygoids referred to Tupilakosaurus by Huene (1959) differ from those of brachyopids, in spite of Huene's contrary statement that they are like those of Batrachosuchus. The expanded cultriform process is not found in any brachyopid; the anterolateral portions of the parasphenoid do not expand around the back of the interpterygoid vacuities as in brachyopids. The atlas referred by Huene (1959) is expanded and smooth anteriorly, unlike that of either Batrachosuchus or Hadrokkosaurus.

Thus although the rear border of the skull of Tupilakosaurus somewhat resembles that of brachyopids, there is so little other evidence of