# A PHYLOGENY OF THE BRACHYOPOIDEA (TEMNOSPONDYLI, STEREOSPONDYLI)

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ABSTRACT—In the thirty years since the last comprehensive review of the Brachyopidae many new brachyopid genera have been described and several different phylogenies proposed. This paper provides revised diagnoses of the Brachyopidae, their sister taxon, the Chigutisauridae, and the Brachyopoidea, erects a new higher taxon, Brachyopomorpha to include stem brachyopoids, and reviews the status of all material referred at one time to these taxa. In it we present revised illustrations of the first described member of the Brachyopidae and clarify parts of the morphology of it and other members of the Brachyopoidea including especially the mandible and postcranial skeleton. A new genus and species, *Vigilius wellesi,* is proposed for the skull of *Hadrokkosaurus bradyi* as the holotype of *H. bradyi,* a mandible, cannot be positively associated with the skull. A phylogenetic analysis including most taxa and all putative outgroups confirms the Chigutisauridae as sister group to the Brachyopidae, forming the Brachyopoidea. *Bothriceps australis* becomes a sister taxon to the Brachyopoidea. *Xenobrachyops allos* and *Keratobrachyops australis* are the most plesiomorphic members of the Brachyopidae and Chigutisauridae respectively.

## INTRODUCTION

The first brachyopid, *Brachyops laticeps,* was described by Owen (in Anon, 1854; Owen, 1855) from the 'sandstone series of Mangali' (=Mangli), India, as a 'labyrinthodont reptile.' Four years later, Huxley (1859) erected a new taxon, *Bothriceps australis* for a second brachyopid whose locality was 'said to be from Australia,' to be followed by Broom (1903) with *Batrachosuchus* sp. (*Batrachosuchus browni* Broom 1915) from the *Cynognathus* Zone of South Africa. The higher taxon, Brachyopidae, was erected by Lydekker (1885) for *Brachyops laticeps.* Since then, many taxa have been included in the family, many have been removed, and several morphological and taxonomic revisions have been carried out. Of these the classic monographs of Watson (1956) and Welles and Estes (1969) reviewed the contents of the Brachyopidae including several taxa not currently considered to be brachyopids. Descriptions of new taxa from Australia (Cosgriff, 1969) and southern Africa (Chernin, 1977) included comprehensive taxonomic revisions. A review and further taxonomic revision of the Australian Brachyopidae was carried out as a preliminary to the present paper (Warren and Marsicano, 1998). The second monophyletic group which we consider as brachyopoid, the Chigutisauridae, was established by Rusconi (1949) for Argentinian taxa variously assigned to the Brachyopidae, the Lydekkerinidae and the Trematosauridae. These specimens have been placed in three species of the chigutisaurid *Pelorocephalus* (Marsicano, 1993a, 1999). Non-Argentinian chigutisaurids are now known from India (Sengupta, 1995), Australia (Warren, 1981a, b; Warren and Hutchinson, 1983; Warren et al., 1997), and South Africa (Warren and Damiani, 1999).

The history of the Brachyopoidea is complex and the following is a review of the principle works only. Säve-Söderbergh (1935) erected the Brachyopoidei and the Brachyopoideae for the single higher taxon Brachyopidae, and the Dvinosauroideae for the single higher taxon Dvinosauridae, but the higher taxon Brachyopoidea correctly is attributed to Lydekker (1885) who first used Brachyopidae as a taxon. The first to add the Chigutisauridae to the Brachyopoidea (Rusconi, 1951) did not consider the position of the Dvinosauridae. Shishkin (1966) included the Brachyopidae (with *Dvinosaurus*), Tupilakosauridae and Metoposauridae in the Brachyopoidea but later (1973) included also the Dvinosauridae. To complicate matters further

Shishkin (1987) placed the Brachyopidae in the Colosteiformes in which he included also the Saurerpetontidae, Trimerorhachidae, Colosteidae and Metoposauridae, but included the Chigutisauridae, with the Zatracheidae and Plagiosauridae, in the Zatracheiformes. Two reviews, Warren (1981b) and Warren and Hutchinson (1983), followed Rusconi (1951) in including the Chigutisauridae in the Brachyopoidea, although in one (Warren, 1981b) the Kourerpetontidae were also considered brachyopids (following Olson and Lammers, 1976). In his most recent review, Shishkin (1991) restricted the Brachyopoidea to the Brachyopidae, Dvinosauridae and Tupilakosauridae.

In early cladistic attempts to establish relationships among these groups Coldiron (1978) and Foreman (1990) were principally concerned with the relationships of the relatives of *Dvinosaurus* from earlier in the Permian but included the brachyopids, while Warren and Hutchinson (1983) did not consider the Dvinosauridae and Tupilakosauridae. Damiani and Warren (1996) used all families previously included in the Brachyopoidea by one or more authors, as well as a single additional terminal taxon from among the stereospondyls. Their analysis showed a monophyletic Brachyopoidea (Brachyopidae + Chigutisauridae) with the Tupilakosauridae and Dvinosauridae as stem-brachyopoids. The only comprehensive cladistic analyses including most temnospondyl higher level taxa as well as brachyopid relatives have been those of Milner (1990) and the computer assisted analysis of Yates and Warren (2000). The former of these analyses excluded the Brachyopidae from the stereospondyls, relating them more closely with *Dvinosaurus* and *Tupilakosaurus* (Fig. 1A), while the latter analysis resulted in a monophyletic Stereospondyli including the Brachyopidae as sister taxon to the Chigutisauridae (Fig. 1B).

The present paper aims to build on the study of Damiani and Warren (1996) in order to elucidate relationships within the Brachyopoidea. As that study was based largely on the literature, in the present analysis an attempt has been made to look at original material wherever possible. All the taxa included in the present analysis have been examined by one or both of the authors. Initially the intention was to confine our analysis to relationships within the Brachyopidae but it has become evident that some of the Australian taxa may be stem brachyopoids rather than brachyopids or chigutisaurids so it became necessary to broaden the analysis to include the Chigutisauridae. The
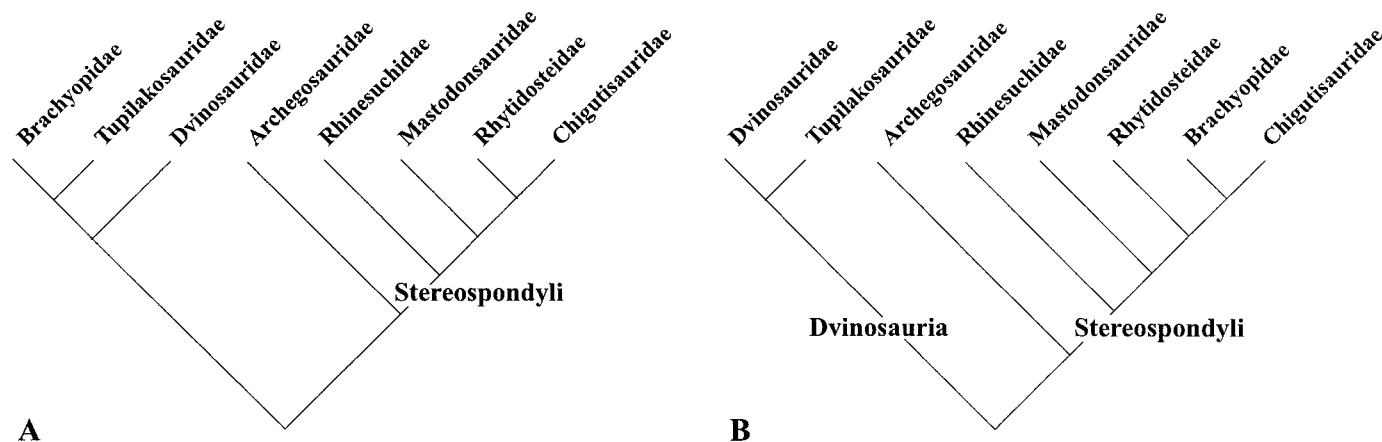
FIGURE 1. Phylogenetic diagrams simplified from those constructed by **A**, Milner (1990) and **B**, Yates and Warren (2000).

election of the outgroups was based on the more inclusive recent analysis that confirmed a sister-group relationship between the brachyopids and chigutisaurids and placed the entire brachyopoid taxon in the stereospondyl clade (Yates and Warren, 2000). The phylogenetic analysis presented below incorporates also data from two chigutisaurid studies, both of which employed cladistic methodology to look at in-group relationships (Sengupta, 1995; Marsicano, 1999).

We provide a revised phylogenetic definition of the Brachyopoidea but follow Yates and Warren (2000) in our definitions of Brachyopidae and Chigutisauridae. A new higher taxon, the Brachyopomorpha, is erected for Brachyopoidea plus taxa which fall on the brachyopoid stem. New diagnoses of the Brachyopoidea, Brachyopidae and Chigutisauridae are accompanied by a review of the status of all material referred at one time to these taxa. This is, in essence, an update of the landmark review of the Brachyopidae (Welles and Estes, 1969) which included comment on the present members of the Chigutisauridae and Dvinosauridae. We adopt Welles and Estes' (1969) format in first listing all taxa which we consider valid members of the Brachyopidae in the order in which they were described. We follow this with Brachyopidae incertae sedis, then taxa removed from the Brachyopidae, followed by a similar listing for the Chigutisauridae and Brachyopoidea. The synonymy lists include only those references in which the taxon name has been changed. It was necessary to include a brief section on brachyopoid morphology, in which we redescribe and reillustrate *Brachyops laticeps,* the first described brachyopid, and document what is known of the brachyopoid postcranial skeleton.

**Institutional abbreviations–AMNH,** American Museum of Natural History, New York, USA; **BM(NH)**, Natural History Museum, London, England; **BP**, Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa; **ISI**, Indian Statistical Institute, Calcutta, India; **MCNA**, Museo de Ciencias Naturales y Antropológicas, Mendoza, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, USA; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN-ZAR**, Zarzaitine collection, Laboratoire de paléontologie, Muséum National d'Histoire Naturelle, Paris; **NMV**, Museum of Victoria, Melbourne, Australia; **NSWGS**, New South Wales Geological Survey, Sydney, Australia; **PIN**, Paleontological Institute, Moscow, Russia; **PVL**, Paleontología de Vertebrados Instituto Miguel Lillo, Tucumán, Argentina; **QM**, Queensland Museum, Brisbane, Australia; **SAM**, South African Museum, Capetown, South Africa; **TsNIGR**, Central Museum for Geological Research and Prospecting, St. Petersburg, Russia; **UCMP**, University of California Museum of Pa-

leontology, Berkeley, USA; **UMZCT**, University Museum of Zoology, Cambridge, England; **UTGD**, University of Tasmania Geology Department, Hobart, Tasmania, Australia; **ZDM**, Zhigong Dinosaur Museum, Zhigong, China.

REVIEW OF BRACHYOPOID TAXA

BRACHYOPOMORPHA, taxon nov.

**Included Taxa**—*Bothriceps australis* and Brachyopoidea.
**Phylogenetic Definition**—A stem-based taxon including *Pelorocephalus* and all taxa closer to it than to *Rhytidosteus.*
**Diagnosis**—Temnospondyl amphibians with the quadrate rami of the pterygoids strongly downturned forming a vaulted palate (inverted U-shaped palate, paralleled in Dvinosauria); quadrate condyles with two parts subequal in size; the exoccipital condyles are rounded and stalked (pedicellate); the ascending ramus of the pterygoid arises from the dorsal surface of the pterygoid as a gently concave lamina; in the mandible, coronoid dentition is restricted to the middle and/or posterior coronoids, the postglenoid area (PGA) is slender and elongated, the prearticular extends posteriorly along the lingual wall of the PGA so that the articular is exposed posterolingually only or completely excluded from the PGA, and the mandibular sulcus of the sensory canal is absent; in the postcranial skeleton, the dorsal process of the clavicle does not develop an anterior flange (paralleled in *Dvinosaurus*).

BRACHYOPOIDEA Lydekker, 1885

**Included Taxa**—Brachyopidae, Chigutisauridae.
**Phylogenetic Definition**—A node-based taxon that includes *Brachyops* and *Pelorocephalus* and all descendants of their most recent common ancestor. This differs from the definition of Yates and Warren (2000) but promotes stability in that the node used marks the dichotomy between the Brachyopidae and the Chigutisauridae.
**Diagnosis**—Brachyopomorph temnospondyls with sensory sulci deeply incised between nostrils and orbits only; presence of a flat cultriform process of the parasphenoid, not anteriorly expanded as in Dvinosauria; in the mandible, articular restricted to a longitudinal tongue on the PGA or completely excluded by a prearticular-surangular suture.

BRACHYOPIDAE Lydekker, 1885

**Included Taxa**—*Xenobrachyops allos, Sinobrachyops placenticephalus, Brachyops laticeps, Vigilius wellesi, Batrachos-*

*uchus henwoodi, Banksiops townrowi, Batrachosuchus browni, Batrachosuchus watsoni, Platycepsion wilkinsoni, Batrachosuchus concordi, Gobiops desertus.*

**Phylogenetic Definition**—A stem-based taxon including all brachyopoids sharing a more recent common ancestor with *Brachyops* than with *Pelorocephalus.*

**Diagnosis**—Brachyopoids with a reduced tooth row on palatines and ectopterygoids; the ascending ramus of the pterygoid is gently concave and lacks a column in its medial part; the otic notch and tabular horns are absent or very reduced; the posttemporal fenestra is as deep as wide, and the maximum width of the interpterygoid vacuity pair is greater than 90% of their length; in the mandible, the postglenoid area (PGA) is extremely elongate and slender and lacks a chordatympanic foramen, the articular is below the level of the dentary tooth row and is restricted to a longitudinal tongue on the PGA, and the prearticular process is absent; in the postcranial skeleton, the rod-like dorsal process of the clavicle slopes posteriorly from its base.

<center>BRACHYOPS LATICEPS (Fig. 2)</center>

*Brachyops laticeps* Owen, in Anon 1854:473
*Brachyops laticeps* Owen 1855:37, plate 2
*Brachyops breviceps* anon. 1854:474 in errore

**Material**—BM(NH) R4414 (holotype), a skull.
**Locality and Horizon**—Mangli (not Mangali, Sengupta, pers. comm., 1998) Beds, Nagpur, Wardha valley, Central India. The Mangli Beds have not been dated by means other than the presence of the single specimen of *B. laticeps* and on that basis were considered Early Triassic (Watson, 1956). Fox (1931) thought them equivalent to the Panchet Formation while Chatterjee and Roy-Chowdhury (1974) suggested stratigraphic equivalence with the upper part of the Kamthi Formation making them Late Permian to Early Triassic. The age of *B. laticeps* is thus far from certain.

**Remarks**—This specimen is the type for the Brachyopidae. It was named, but not described, in the abstract of a paper presented by Owen to a meeting of the Geological Society of London. The abstract was written by an anonymous author who incorrectly referred to the species as *Brachyops breviceps* (Anon, 1854) but the full description with illustrations appeared the following year (Owen, 1855). Unfortunately the specimen is badly preserved with fragile bone which precludes further preparation. Missing areas noted in the text were restored by Welles and Estes (1969) to conform with the pattern in other brachyopids. The specimen is especially poorly preserved in the antorbital region and the occiput, which preserves neither sutures nor any internal details of skull morphology. We have re-examined the specimen and provide new figures (Fig. 2) in which the unknown areas are not restored, and a brief redescription (below). We disagree with the previous reconstruction (Welles and Estes, 1969:fig. 15) in the following details: the exoccipitals do not appear to contact the pterygoids on the posterior margin of the palate; the presence or absence of an upper or lower palatoquadrate fissure is not determinable; and no sensory sulci are preserved between the orbits and nostrils. Neither quadrates nor mandibles are present.

**Taxonomic Position**—Brachyopidae.

<center>PLATYCEPSION WILKINSONI</center>

*Platyceps wilkinsoni* Stephens 1887:1118, pl. XXII
*Bothriceps wilkinsoni* Lydekker 1890:172
*Platyceps wilkinsoni* Romer 1947:235
''*Platyceps*'' *wilkinsoni* Watson 1956:338, fig. 11, pl. 39
*Platycepsion wilkinsoni* Kuhn 1961:79
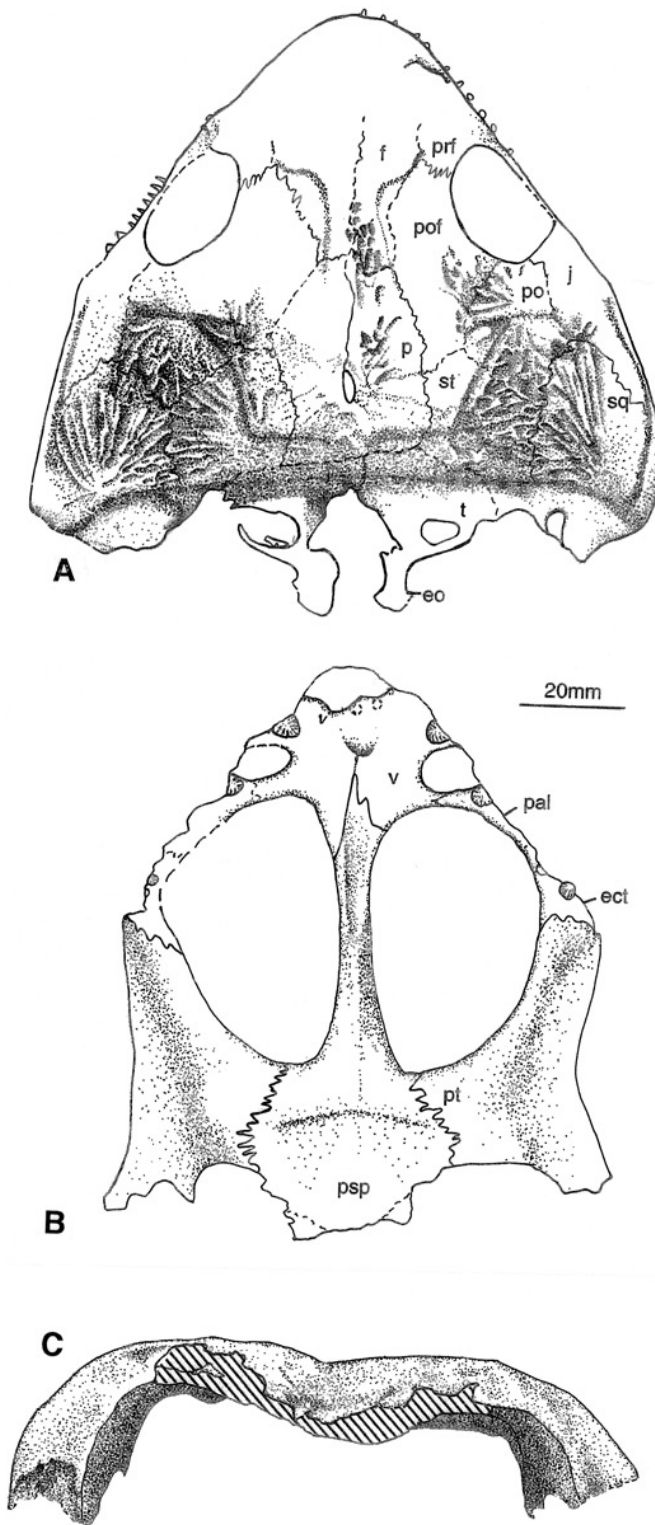*Blinasaurus wilkinsoni* Cosgriff 1969:68, fig. 3



FIGURE 2. *Brachyops laticeps* Owen, BM(NH) R4414. Drawings of the skull in **A**, dorsal; **B**, ventral; and **C**, occipital views. Cross-hatching in C represents matrix. **Abbreviations**: **ect**, ectopterygoid; **eo**, exoccipital; **f**, frontal; **j**, jugal; **p**, parietal; **pal**, palatine; **po**, postorbital; **pof**, postfrontal; **prf**, prefrontal; **psp**, parasphenoid; **pt**, pterygoid; **sq**, squamosal; **t**, tabular; **v**, vomer.

*Bothriceps wilkinsoni* Welles and Estes 1969:21
*Platycepsion wilkinsoni* Shishkin 1973:16
*Blinasaurus wilkinsoni* Chernin 1977:88
*Platycepsion wilkinsoni* Warren and Marsicano 1998:333, fig. 2

**Material**—NSWGS F12572 (holotype), an immature individual consisting of the dorsal skull roof, fragments of mandible and ceratobranchials, an articulated pectoral girdle and a vertebral column consisting of 22 poorly ossified segments.

**Locality and Horizon**—Terrigal (Gosford) Formation, Narrabeen Group, Railway Ballast Quarry, near Gosford, New South Wales, Australia. The Australian Phanerozoic timescale (Young and Laurie, 1996) shows the Narrabeen Group extending from Late Permian into the early Anisian. As the Terrigal Formation forms the uppermost unit of the Narrabeen Group, the position of the fauna is latest Spathian or very early Anisian.

**Remarks**—The specimen is in poor condition and is a juvenile that cannot be distinguished taxonomically from other brachyopids except in the contact between the postorbital and parietal, a character nevertheless sufficiently distinct to permit generic separation. This character is found elsewhere only in the Dvinosauria (sensu Yates and Warren, 2000) which also are usually perennibranchiate. In the Dvinosauria, however, the number of presacral vertebrae is usually increased (Warren, 1999). *Platycepsion* was recently reviewed by Warren and Marsicano (1998) who concluded that it was a brachyopid for the following reasons: the specimen appears to have had a deep skull with posteriorly protruding condyles, lacks tabular horns, has a convex margin of the occipital portion of the squamosal, has an elongate postglenoid area of the mandible, and the pectoral girdle is narrow. The specimen is excluded from the analysis because of its juvenile nature and because the palate and detail of the occiput are not preserved.

**Taxonomic Position**—Immature Brachyopidae

### BATRACHOSUCHUS BROWNI

*Batrachosuchus browni* Broom 1903:499, figs. 1, 2

**Material**—SAM K5868 (holotype), a skull. Other material from the same horizon is considered as *Batrachosuchus* sp. (below), and is used in the matrix to provide mandibular characters for both *B. browni* and *B. watsoni*.

**Locality and Horizon**—Aliwal North locality, Cape Province, South Africa, *Cynognathus* Zone, Early-Middle Triassic.

**Remarks**—*B. browni* was redescribed by Chernin (1977) who followed Welles and Estes (1969) in separating it and *B. watsoni*. In common with most brachyopids the antorbital region is incompletely preserved. The specimen is discussed further under *B. watsoni*.

**Taxonomic Position**—Brachyopidae.

### BATRACHOSUCHUS WATSONI (Fig. 3E)

*Batrachosuchus* sp. Watson 1919:44, figs. 27, 28
*Batrachosuchus watsoni* Haughton 1925:17

**Material**—BM(NH) R3589 (holotype), a skull.

**Locality and Horizon**—Although the locality for *B. watsoni* is unknown it is assumed to have been recovered from the Burghersdorp district (Watson, 1956), Cape Province, South Africa, *Cynognathus* Zone, Early-Middle Triassic.

**Remarks**—This is an extremely well preserved brachyopid skull and the one which best represents the characters of the derived members of the Brachyopidae. It is remarkable also for the preservation, on both sides of the skull, of a bone in the position of a columella. The species was erected by Haughton (1925) for a specimen described (Watson, 1919) as *Batrachosuchus* sp. Haughton considered *B. watsoni* differed from *B. browni* in that it was wider, lacked an interfrontal, and the par-

asphenoid 'passes further back.' Watson redescribed the specimen in 1956. Welles and Estes (1969) followed Haughton in separating the species on the basis of skull proportions, largely related to the greater skull breadth in *B. watsoni*. Chernin (1977) in her description of *B. browni* added four further morphological differences: the presence of a vomerine foramen in *B. browni*, the fact that the parasphenoid does not reach the posterior border of the palate, and the fact of the narrower lateral line canals in *B. browni*. We do not agree that the species should be separated on the basis of such small differences in skull proportions. The vomerine depression in *B. watsoni* we consider the homologue of the foramen in *B. browni*, which may in fact be a depression filled with sediment. The different widths of the sensory canals is somewhat subjective. *B. browni* has an interfrontal, a midline bone which appears occasionally in apparently unrelated taxa (e.g., *Lydekkerina, Trematosuchus, Eryops*) (Shishkin and Welman, 1994). The separation of the exoccipitals by the parasphenoid appears to be a good character and we have scored it in our matrix. The two species appeared as sister taxa in our phylogenetic analysis and we suggest that *B. watsoni* may be a junior synonym of *B. browni*.

**Taxonomic Position**—Brachyopidae.

### BATRACHOSUCHUS SP.

*Batrachosuchus* sp. Watson 1956:336, figs. 9, 10

**Material**—UMZCT 194, mandibular fragment; UMZCT 193, atlas.

**Locality and Horizon**—Farm Luiper Kop, between Bhurgersdorp and Knapdaar, Orange Free State, South Africa.

**Remarks**—Watson described the articular and postglenoid area of a right mandibular ramus, comparing them with the only 'brachyopid' mandibles known at that time (*Bothriceps, Pelorocephalus, Dvinosaurus* and *Eobrachyops*) of which only *Bothriceps* remains in the Brachyopidae. Brachyopid features of the postglenoid area include the exclusion of the articular from the lingual surface, the angular extending to the posterior end of the PGA, and the lack of a chorda tympanic foramen. Watson suggested that an atlas found with the ramus was likely to be brachyopid also, as remains of labyrinthodont fragments are rare in the *Cynognathus* Zone, justifying association of fragments found close together. The atlas has an anteroposteriorly elongate centrum which is characteristic of brachyopids. Both fragments were referred to ?*Batrachosuchus* which was the only known South African brachyopid (Watson, 1956).

**Taxonomic Position**—*Batrachosuchus* sp., Brachyopidae.

### BATRACHOSUCHUS SP.

*Batrachosuchus* sp. Welles and Estes 1969:47, figs. 23, 24, 25
*Batrachosuchus* sp. Colbert and Cosgriff 1974:figs. 10, 13

**Material**—UCMP 42856 (Welles and Estes, 1969), cranial fragments, atlas, axis. This material has now been renumbered as follows: UCMP 42856, UCMP 140568–69, UCMP 140571–72, UCMP 140575–78, UCMP 140586, cranial fragments; UCMP 140587–92, mandibular fragments; UCMP 80857, atlas; UCMP 80858, axis; UCMP 140580, neural arch; UCMP 42856, 20 crescentic intercentra; UCMP 42856, pleurocentrum; UCMP 140584 interclavicular fragment; UCMP 140570, 140573–74, 140583, 140585, clavicular fragments; UCMP 80859, 80860, humeri.

**Locality and Horizon**—Collected in 1947 by Peabody and Camp from UCMP Locality V 4747, Bethel Farm (presumably the Bethel near Rouxville) Orange Free State, South Africa. *Cynognathus* Zone, Early-Middle Triassic.

**Remarks**—The material consists of undoubted brachyopid mandibular rami, brachyopid cranial material (Colbert and Cos-
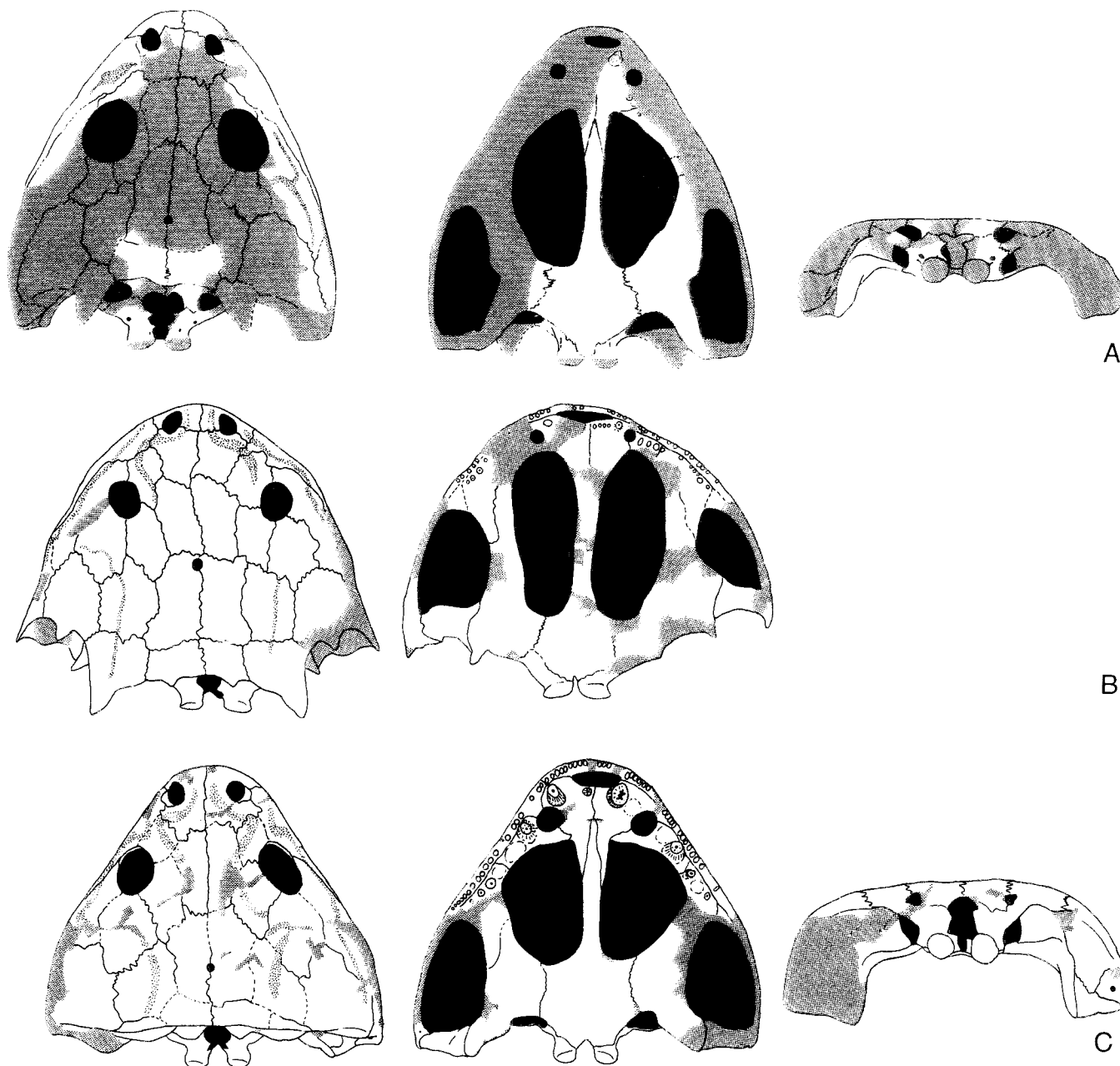
FIGURE 3.    Line drawings of the more complete brachyopoid skulls, and of their sister group, *Bothriceps australis*. **A**, *Bothriceps australis* (redrawn from Warren and Marsicano, 1998), the holotype, and a cast (some sutures are clearly visible as impressions on the skull roof although the bone is missing). **B**, *Compsocerops cosgriffi* (redrawn from Sengupta, 1995). **C**, *Xenobrachyops allos* (redrawn from Damiani and Warren, 1996), and the holotype. **D**, *Vigilius wellesi* (redrawn from photographs in Welles and Estes, 1969, a cast, and from notes of both authors). **E**, *Batrachosuchus watsoni* (redrawn from Watson, 1956), and from notes of both authors. **F**, *Banksiops townrowi* (redrawn from Cosgriff, 1974, and from notes of both authors) (the skull is dorsoventrally flattened so most of the occiput is obscured). Gray shading/stippling represents areas of missing bone; sensory sulci stippled manually; fenestrae, vacuities and foramina are blackened. Not to scale.

griff, 1974), and postcranial elements. An axis, atlas, intercentra and a humerus have been described (Welles and Estes, 1969), and pectoral girdle material remains undescribed.

Although this material represents the remains of at least five individuals (four right articular portions of the mandible, five left clavicles) none of it was found in articulation. Despite this it is reasonable to refer it all to the Brachyopidae as all of the identifiable elements pertain to that taxon. This is important as brachyopid postcranial material is rare, the only articulated material being two specimens from the Syd-

ney Basin. One of these, *Platycepsion wilkinsoni,* is a poorly-preserved juvenile specimen and the other is in private hands and undescribed.

All of the material was treated as brachyopid and referred to *Batrachosuchus* sp. especially because a transverse groove at the back of the postparietals just below their downward flexure was said to be identical with that of *B. watsoni* (Welles and Estes, 1969). This is undoubtedly true but appears to be a feature of all brachyopids in which that area is preserved. This material, like Watson's (above) is likely from *Batrachosuchus*
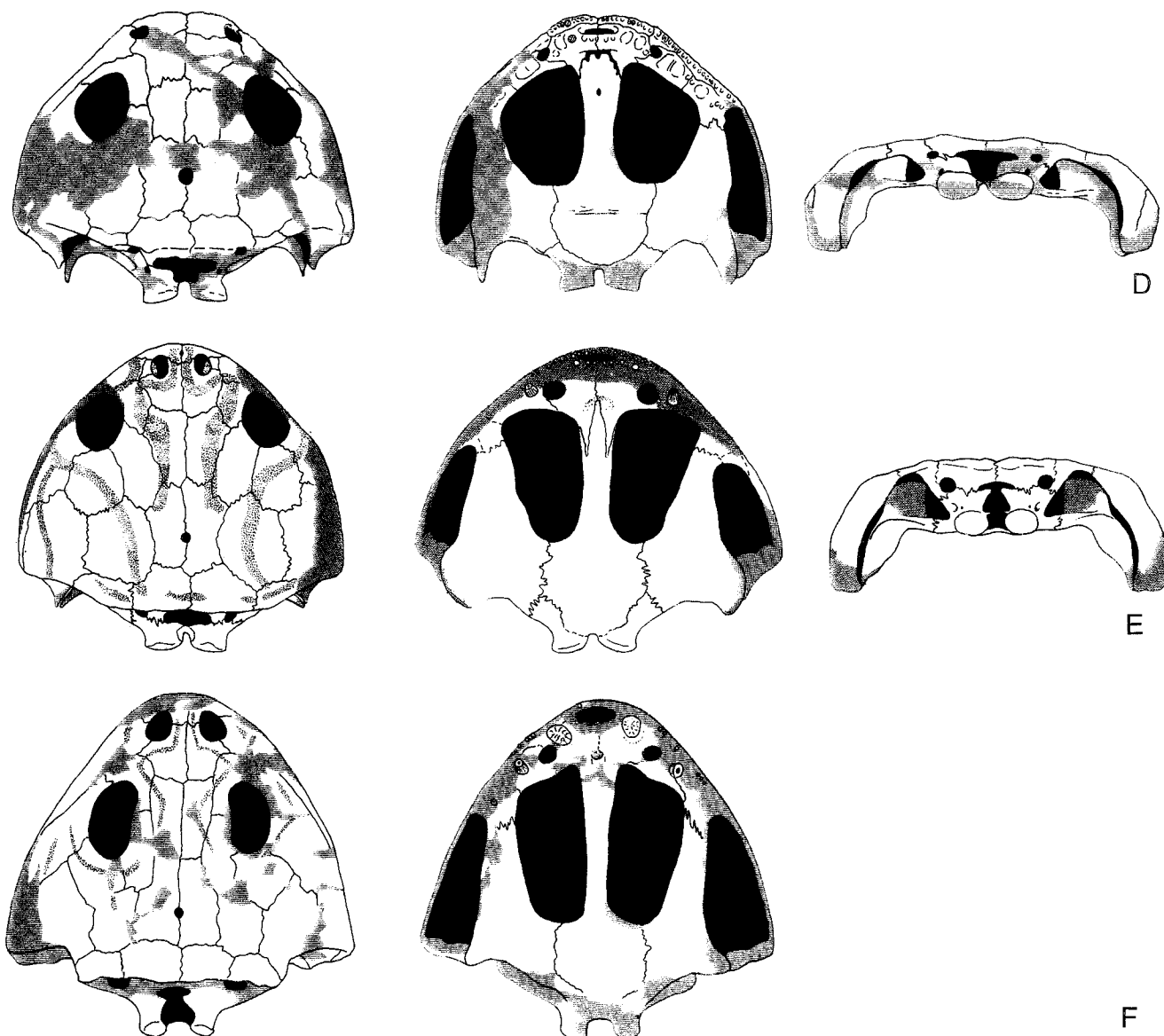
FIGURE 3. Continued.

and we have treated it as such, using it to supplement the *Batrachosuchus* characters in our matrix.

**Taxonomic Position**—*Batrachosuchus* sp., Brachyopidae.

### BATRACHOSUCHUS HENWOODI

*Blinasaurus henwoodi* Cosgriff 1969:68, figs. 4–8
*Batrachosuchus henwoodi* Warren and Marsicano 1998:336, fig. 3

**Material**—WAM 62.1.42 (holotype), a skull; UCMP 61065, 61069, 61142, mandibular rami; UCMP 61078, 61086, 61093, clavicular fragments.

**Locality and Horizon**—UCMP Locality V6046, north of Blina Homestead, approximately 100 km ESE of Derby, Western Australia. Blina Shale, Early Triassic.

**Remarks**—As with most material from the Blina Shale, the skull of *B. henwoodi* is preserved as a partial mould of the internal surfaces of the skull bones with the result that the skull margins are lost. Cosgriff described mandibular material from nearby localities as from the same taxon as the skull and we concur that this is likely as no other brachyopids are known from the Blina Shale. *B. henwoodi* was placed in *Batrachosuchus* (Warren and Marsicano, 1998) after *Blinasaurus* became unavailable. They considered the much larger size of the orbits as sufficient reason for specific separation from *Batrachosuchus browni*.

**Taxonomic Position**—Brachyopidae.

### BATRACHOSUCHUS CONCORDI

*Batrachosuchus concordi* Chernin 1977:90, fig. 1

**Material**—BP/1 F3728 (holotype), a skull with associated mandible and postcranial remains.

**Locality and Horizon**—Locality 15 (Drysdall and Kitching, 1963), N'taweri Formation, Upper Luangwa Valley, Zambia. Middle Triassic.

**Remarks**—The material consists of a small skull, right mandibular ramus, and elongate atlas and axis. Other postcranial

material associated with *B. concordi* by Chernin (1977) is unlikely to be amphibian.

The skull is of brachyopid proportions, has a palatoquadrate fissure, straight medial border to the subtemporal vacuity, and a broad cultriform process. The sensory canal system is unusually deeply impressed into the more posterior skull bones. Of note is the fact that the skull is small, the orbits extremely large and the sutures do not interlock, indicating its probable juvenile nature. For this reason it was excluded from the phylogenetic analysis but is included in the matrix.

**Taxonomic Position**—Immature Brachyopidae.

*VIGILIUS* gen. nov.

**Type Species**—*Vigilius wellesi* gen. et sp. nov. This is the only species in the genus.

**Etymology**—From the Latin *vigilia,* keeping watch. Refers to the large orbits of Welles' original name and also to the fact that the skull was keeping vigil over the Grand Canyon, Arizona.

**Diagnosis**—A large stereospondyl skull which differs from members of the Brachyopidae as follows; nares and orbits widely separated; orbits proportionally larger than all brachyopids except *Batrachosuchus henwoodi* (Cosgriff, 1969); anterior end of the cultriform process unusually wide; vomerine plate anterior to the interpterygoid vacuities unusually narrow; lateral cheek margins of the quadratojugals probably emarginated. A full description of the holotype skull appeared in Welles and Estes (1969).

*VIGILIUS WELLESI* gen. et sp. nov.
(Fig. 3D)

*Taphrognathus bradyi* Welles 1947:246, figs. 3–6
*Hadrokkosaurus* Welles 1957:982
*Hadrokkosaurus bradyi* Welles and Estes 1969:30, figs. 19–22, 26–27

**Holotype**—UCMP 36199, a skull.

**Other Material**—UCMP 36205, 36247, 36836, 37771, 75431, 75432, 75433, 75435, 76477, 76478, 76479, isolated skull fragments; UCMP 36205, mandible; UCMP 80855, atlas; UCMP 36841, clavicle; UCMP 37770, humerus.

**Locality and Horizon**—UCMP 36199, the skull and holotype of *Vigilius wellesi,* is from UC V4207, Cameron-Grand Canyon Highway, Holbrook Member of the Moenkopi Formation, Early-Middle Triassic. The other material is from UC V3922, 10 km west of Holbrook, Arizona, USA. Holbrook Member of the Moenkopi Formation, Early-Middle Triassic.

**Etymology**—Named in honour of the late Dr. Sam Welles who first named the genus and described the skull with the late Dr. Richard Estes.

**Diagnosis**—As for the genus.

**Remarks**—In 1969, Welles and Estes referred this skull to *Hadrokkosaurus bradyi,* a genus and species based on a right mandibular ramus which may be brachyopoid but has features found in no other brachyopoids (see Brachyopoidea incertae sedis, below). The skull and mandibular ramus are from different sized animals and from localities over 160 km apart. It is necessary therefore to leave the name *Hadrokkosaurus bradyi* associated with the holotype ramus only (UCMP 36199), and to designate a new name, *Vigilius wellesi,* for the skull. Scrap postcranial material associated with the holotype of *V. wellesi* appears to be brachyopoid and is here transferred to the replacement name, *Vigilius wellesi.* An isolated pterygoid assigned to *Hadrokkosaurus* (=*Vigilius*), UCMP 36247 (Colbert and Cosgriff, 1974; originally described as a scapulocoracoid by Welles, 1947) differs from the usual brachyopid pterygoid as seen in *Batrachosuchus* sp. (Colbert and Cosgriff, 1974) in that it has

a marked ridge on the ascending ramus of the pterygoid lateral to the position of the dorsal column in chigutisaurids, and a thickened margin of the medial border of the pterygoid. This area was thought to be the area for articulation with the exoccipital (Colbert and Cosgriff, 1974) but it is not present in other brachyopids. Despite the large size of the skull, Welles and Estes thought it could be immature because of poor cranial suturing and its large orbits, and because fragments from the Holbrook quarry were from an individual half as large again.

Shishkin (1973) considered *V. wellesi* a *Dvinosaurus* relative, later assigning it (1991) to the Dvinosauridae. Our analysis does not support Shishkin's suggestion but if, as suggested by our analysis, *Batrachosuchoides* is a dvinosaur, then *Vigilius* becomes the only non-Gondwanan brachyopid representative before the Jurassic. The dvinosaurian affinities of *Vigilius* need further investigation. The extreme width of the anterior part of the cultriform process of the parasphenoid is shared with *Dvinosaurus* and the Tupilakosauridae. Other characters shared with these taxa are the extreme narrowness of the vomerine plate anterior to the cultriform process and the widely separated nares. The isolated ascending ramus of the pterygoid (UCMP 36247—above) is morphologically closer to that of *Dvinosaurus* than brachyopids in that it is thickened medially and is traversed by a marked ridge which is more lateral than the dorsal column of chigutisaurs. The ascending ramus of the pterygoid in the skull of *V. wellesi* looks more typically brachyopid but is obscured by matrix internally. As restored (Welles and Estes, 1969) it terminates far from the midline as it does in *Dvinosaurus* and Tupilakosauridae. This last character is no doubt related to that noted by Shishkin (1991), that the apex of the pterygoid plate lies below the tabular. Given the above evidence we are inclined to support Shishkin's view that *Vigilius* is a dvinosaur. The fact that in our analysis it is nested within the Brachyopidae may reflect the over-restoration of the specimen and our lack of knowledge of the distal parts of the ascending ramus of the pterygoid.

**Taxonomic Position**—? Brachyopidae.

*XENOBRACHYOPS ALLOS*
(Fig. 3C)

*Brachyops allos* Howie 1972:270, figs. 1–3
*Xenobrachyops allos* Warren and Hutchinson 1983:59
*Xenobrachyops allos* Damiani and Warren 1996:fig. 8

**Material**—QMF 6572 (holotype), a skull; QMF 10118–9, partial mandible; QMF 39651, fragmentary interclavicle; QMF 39652, fragmentary clavicle.

**Locality and Horizon.** Queensland Museum field locality L215, Duckworth Creek, near Bluff, Queensland. Arcadia Formation, Rewan Group, Early Triassic.

**Remarks**—A brachyopid mandible from the same site as the holotype appears to be from the same specimen (Warren, 1981b). This well-preserved skull is plesiomorphic in several characters in relation to other brachyopids. The medial wall of the subtemporal vacuity is not parallel to the skull midline, the quadrate and ascending ramus of the pterygoid are sutured to the squamosal (palatoquadrate fissure absent), and the quadrate ramus of the pterygoid does not project posterior to the skull. A redescription (Damiani and Warren, 1996) included a small unornamented LEP (lateral exposure of the palatine) on the internal part of the lateral margin of the orbit and a septomaxilla. The LEP is absent in the ingroup except in *Batrachosuchoides* in which it is large and ornamented.

An autapomorphy of the taxon is the extreme retraction of the palatine ramus of the pterygoid so that the ectopterygoid forms a large part of the strut between the subtemporal and interpterygoid vacuities.

**Taxonomic Position**—Basal member of the Brachyopidae.

*BANKSIOPS TOWNROWI*
(Fig. 3F)

*Blinasaurus townrowi* Cosgriff 1974:7, figs. 1–29
*Banksia townrowi* Warren and Marsicano 1998:338
*Banksiops townrowi* Warren and Marsicano 2000

**Material**—UTGD 87785 (holotype), a skull; and a large amount of unassociated material from five different localities.

**Locality and Horizon**—Old Beach Locality, approximately 17 km north-west of Hobart, Knocklofty Formation, Early Triassic.

**Remarks**—The genus name *Banksia* was erected for *Blinasaurus townrowi* when the name *Blinasaurus* became invalid following the transfer of the holotype of the genus *Blinasaurus* to *Platycepsion* (Kuhn, 1961). As the name *Banksia* was preoccupied by an arachnid (Voigts and Oudermans, 1905) we renamed the specimen *Banksiops* (Warren and Marsicano, 2000). *Banksiops townrowi* is typically brachyopid but is clearly distinct from all other brachyopids in its marked squamosal embayment.

**Taxonomic Position**—Brachyopidae.

*SINOBRACHYOPS PLACENTICEPHALUS*

*Sinobrachyops placenticephalus* Dong 1985:2, figs. 1–2

**Material**—ZDM 1 (holotype), a skull, and undescribed mandibular and postcranial material.

**Locality and Horizon**—Zhigong Dashanpu County, Sichuan Province, Lower Shaximiao Formation, Middle Jurassic.

**Remarks**—This material includes an undescribed mandible which has not been seen by either author. The skull was examined by the senior author and our characters are scored from drawings made at that time. A redescription of the skull and a description of all associated material is planned jointly with Professor Dong who agreed that we could use the cranial material in our analysis. We consider the specimen has paired nares rather than a single medial nostril as originally described (Dong, 1985); the lateral margins of both nares are preserved but the area between them is restored. *Sinobrachyops* occupies a position as sister group to all brachyopids except *Xenobrachyops* because it retains a paraquadrate foramen, its posttemporal fenestra is wider than deep and it has a continuous palatal tooth row.

**Taxonomic Position**—Brachyopidae.

*GOBIOPS DESERTUS*

*Gobiops desertus* Shishkin 1991:79, figs. 1–13

**Material**—PIN4174/102 (holotype), a squamosal; PIN4174/101, clavicle; PIN4174/104–105, mandibular fragments; PIN4174/110, clavicle; PIN4174/111, clavicle; PIN4174/113, humerus; PIN4174/114, atlas; PIN4174/116–117, PIN4174/123–124, intercentra.

**Locality and Horizon**—Shar Teg, southwestern Mongolia. Shar Teg Beds, Late Jurassic.

**Remarks**—These remains are fragmentary but appear to be brachyopid because of the rounded, posteriorly projected exoccipital condyles and lack of a tabular horn, although the dorsal process of the clavicle is unusually low for that group (Shishkin, 1991). *Gobiops* is unusual among brachyopids in that some of the centra are stereospondylous, but such centra are present also in the post-Triassic *Ferganobatrachus* and in the chigutisaurid, *Koolasuchus* (Warren et al., 1997). The cranial material is too fragmentary to be included in the matrix.

**Taxonomic Position**—Brachyopidae.

BRACHYOPIDAE indet.

Brachyopidae gen. et sp. indet Watson 1958:259, fig. 16

**Material**—BM(NH)R 9586, partial skull of a very large specimen.

**Locality and Horizon**—Quarry (now filled) at St. Peters, Sydney, New South Wales, Australia. Ashfield Shale of the Wianamatta Series, Middle Triassic.

**Remarks**—The partial skull is unquestionably brachyopid (Watson, 1958) through its downturned quadrate ramus of the pterygoid with a straight medial border to the subtemporal vacuity and apparent absence of a tabular horn. Watson noted the unusually wide deeply-impressed lateral line groove (sensory canal) on the supratemporal. Deep sensory canals are characteristic of brachyopoids where they are usually deepest in the preorbital area; they are also deep in the postorbital region of *Batrachosuchus watsoni* (Watson, 1956).

**Taxonomic Position**—Brachyopidae.

Brachyopidae Jalil 1994:1, figs. A–E

**Material**—MNHN-ZAR 55–56, cranial fragments.

**Locality and Horizon**—Lower Sandstone, Lower Zarzaitine Formation, Algeria. Middle Triassic.

**Remarks**—This material, comprising a fragment of occiput, a second skull roof fragment, and teeth, was placed by Jalil (1994) in the Brachyopidae. He suggested that it could represent a new species of *Hadrokkosaurus* (=*Vigilius*). Jalil used a process of elimination in his study and we agree that the material appears to be brachyopid.

**Taxonomic Position**—Brachyopidae.

Brachyopidae Damiani and Warren 1996:285, figs. 5–69

**Material**—QMF 14483, right mandibular ramus.

**Locality and Horizon**—Queensland Museum locality L778 near Glenidal Homestead, south east of Rolleston, Queensland. Glenidal Formation, which lies above the Arcadia Formation, Rewan Group, Early Triassic.

**Remarks**—An isolated but complete right mandibular ramus that represents the most completely known brachyopid lower jaw.

**Taxonomic Position**—Brachyopidae.

BRACHYOPIDAE incertae sedis

*NOTOBRACHYOPS PICKETTI*

*Notobrachyops picketti* Cosgriff 1967 nomen vanum
*Notobrachyops picketti* Cosgriff 1973:figs. 1–2

**Material**—NSWGS F8258 (holotype), skull table.

**Locality and Horizon**—Hurstville Brick Company quarry, Mortdale, New South Wales. Ashfield Shale, Wianamatta Group, Middle Triassic.

**Remarks**—This taxon was excluded from our analysis because few characters could be scored for it. Although small, the specimen appears to be adult because its pineal foramen is small. As pointed out previously (Warren and Marsicano, 1998) the specimen is unusual for a brachyopoid in that it lacks sensory canals but is brachyopoid in the presence of posterior projections of the squamosal and pterygoid indicating the presence of a squamosal-quadratojugal trough. If brachyopoid it belongs with the Brachyopidae because it has no tabular horn.

**Taxonomic Position**—Brachyopidae incertae sedis.

*BATRACHOSUCHOIDES LACER*

*Batrachosuchoides lacer* Shishkin 1966:310
*Batachosuchus lacer* Welles and Estes 1969:23

*Batrachosuchoides lacer* Shishkin 1973:75

**Material**—PIN953/2 (holotype), an antorbital region; PIN953/3, PIN953/8–12, PIN953/15–16, PIN953/28, PIN953/31–33, PIN953/35, cranial and mandibular fragments and postcranial remains from several localities.

**Locality and Horizon**—Federov Horizon, Baskunchakskaia Series, Viatki Basin, Russia. Early Triassic.

**Remarks**—Welles and Estes (1969) noted that it is difficult to differentiate *Batrachosuchoides* from *Batrachosuchus,* a situation exacerbated by *Batrachosuchoides* being represented only by the antorbital region which is badly preserved or missing in all *Batrachosuchus* specimens. Mandibular material in the collections at the PIN (PIN 1584/9, 1584/10) although weathered, appears to be brachyopid rather than dvinosaur (Shishkin 1973, plate IX—2,3). Other mandibular material (PIN 1584/9) in the collection appears to be brachyopid in that a tongue of articular is exposed on the dorsal surface of the post glenoid area between the surangular and the prearticular.

The skull fragment is of interest as that area is rarely preserved in brachyopids. It has a septomaxilla, a large, ornamented lateral exposure of the palatine bone (=palatolacrimal of Shishkin, 1966) and, on a second fragment, an ossified basioccipital, and exoccipital condyles which are underplated by the parasphenoid. All of these primitive characters are found also in Dvinosauria (Yates and Warren, 2000). The tusks are extremely large as they are also in Tupilakosauridae and *Dvinosaurus.* The marginal teeth decrease in size anterior to the anterior palatal vacuity, a character used previously (Warren and Hutchinson, 1983) to indicate brachyopid affinity. Also brachyopid are the closely spaced nares, deeply incised sensory canals and enlarged foramen on the exoccipital for nerve X. Associated material includes a typical brachyopid quadrate and an ilium (PIN 953/35) with an extremely long, blade. Also associated are 'ribs' which may in fact be ceratobranchials as Shishkin (1966) likens them to the 'ribs' of *Tupilakosaurus* which are now thought to be ceratobranchials (Warren, 1999). The presence of ossified ceratobranchials in the adult may be characteristic of the Dvinosauria (Warren, 1999). Because of its fragmentary nature *Batrachosuchoides* was excluded from the final phylogenetic analysis although included in the data matrix. In preliminary analyses it clustered with the Tupilakosauridae + *Dvinosaurus* more often than with the Brachyopidae. Until more complete material is available we consider it parsimonious to leave it in Brachyopidae incertae sedis, because mandibular rami associated with it are brachyopid.

**Taxonomic Position**—Brachyopidae incertae sedis.

## TAXA REMOVED FROM THE BRACHYOPIDAE

**Taxa Removed by Welles and Estes (1969)**

*DVINOSAURUS PRIMUS* Amalitzki, 1921

**Taxonomic Position**—Dvinosauridae (Amalitzki, 1921).

*PHRYNOSUCHUS WHAITSI* Broom, 1913

**Taxonomic Position**—*Rhinesuchus* sp. indet. (Chernin and Kitching, 1977).

*TUNGUSSOGYRINUS BERGI* Efremov, 1939

**Taxonomic Position**—Branchiosauridae (Shishkin 1998).

*BOREOSAURUS THORSLANDI* Nilsson, 1943

**Taxonomic Position**—Indeterminate temnospondyl mandibular core.

*PELOROCEPHALUS MENDOZENSIS* Cabrera, 1944

**Taxonomic Position**—Chigutisauridae (Reig, 1961).

*TUPILAKOSAURUS HEILMANI* Nielsen, 1954

**Taxonomic Position**—Tupilakosauridae (Kuhn, 1961).

*ENOSUCHUS BREVICEPS* Efremov in Konzhukova, 1955

**Taxonomic Position**—Seymouriamorpha (Shishkin, 1973).

*PLAGIOROPHUS PARABOLICEPS* Konzhukova, 1955

**Taxonomic Position**—Plagiosauridae (Shishkin, 1987).

*EOBRACHYOPS TOWNENDI* Watson, 1956
(=*Isodectes obtusus* Sequeira, 1998)

**Taxonomic Position**—Saurerpetontidae (Sequeira, 1998).

*INDOBRACHYOPS PANCHETENSIS* Huene and Sahni, 1958

**Taxonomic Position**—Rhytidosteidae (Warren and Black, 1985).

**Taxa Removed from the Brachyopidae Elsewhere**

*BOTHRICEPS MAJOR* Woodward, 1909

**Taxonomic Position**—*Trucheosaurus major,* Rhytidosteidae (Marsicano and Warren, 1998).

*KOURERPETON BRADYI* Olson and Lammers, 1976

**Taxonomic Position**—Tupilakosauridae (Warren, 2000).

**Taxa Removed from the Brachyopidae in this Paper**

*BOTHRICEPS AUSTRALIS*
(Fig. 3A)

*Bothriceps australis* Huxley 1859:39, pl. 2

**Material**—BM(NH) R23110 (holotype), skull and mandible in articulation.

**Locality and Horizon**—The specimen is of unknown locality and horizon but 'said to be from Australia.' If Australian, circa 1859, it is most likely to have been collected in the Sydney Basin and, if so, could be from the Late Permian or the Triassic.

**Remarks**—The preserved skull roof is largely an internal mould with the result that the sutures are clearly visible in most areas. Unfortunately the antorbital region retains the bone so that the sutures are less clear in that region. The presence of a lacrimal as restored by Watson (1956) cannot be confirmed. In addition the mandible conceals much of the skull margin and maxillary and palatal tooth rows.

Although we scored the tabular horns as not determinable we think that they may have been present as the posterior margin of the core of the tabulars projects and the paroccipital processes are angled slightly posteriorly as though a tabular horn were present. An otic embayment may have been present also.

**Taxonomic Position**—Brachyopomorpha taxon nov. In our phylogenetic analysis this taxon is the sister group to the Brachyopoidea. We erected the taxon Brachyopomorpha to include Brachyopoidea and those taxa on the brachyopid stem (closer to Brachyopoidea than to Rhytidosteidae).

*AUSTROBRACHYOPS JENSENI* nomen dubium

*Austrobrachyops jenseni* nomen dubium Colbert and Cosgriff 1974:5, figs. 1, 4, 5, 8, 12

**Material**—AMNH 9346 pterygoid.
**Locality and Horizon**—Coalsack Bluff, Transantarctic

Mountains, Antarctica (AMNH 9346), Graphite Peak, Transantarctic Mountains, Antarctica (AMNH 9301). Lower Fremouw Formation, Early Triassic.

**Remarks**—The holotype (AMNH 9346) was described as a brachyopid pterygoid (Colbert and Cosgriff, 1974). It is not demonstrably amphibian and may belong to the Dicynodontida.

**Taxonomic Position**—Tetrapoda indet.

CHIGUTISAURIDAE Rusconi, 1949

**Included Taxa**—*Keratobrachyops australis, Kuttycephalus triangularis, Compsocerops cosgriffi, Siderops kehli, Pelorocephalus* species, *Koolasuchus cleelandi.*

**Definition**—A stem-based taxon including all brachyopoids sharing a more recent common ancestor with *Pelorocephalus* than with *Brachyops.*

**Diagnosis**—Brachyopoid amphibians with a substapedial ridge on the dorsal surface of the pterygoid corpus; the ascending ramus of the pterygoid is gently concave and posteriorly recurved in vertical section; in the mandible, the posterior meckelian foramen is bordered by the prearticular and postsplenial exclusively.

*PELOROCEPHALUS MENDOZENSIS*

*Pelorocephalus mendozensis* Cabrera 1944:423, fig. 2
*Chigutisaurus tunuyanensis* Rusconi 1948:226, fig. 1
*Pelorocephalus mendozensis* Marsicano 1999:figs. 1–6

**Material**—MLP 44-VII-5-1 (holotype), skull with mandible; MCNA 2660, partial skull and mandible; PVL 3531, skull; AMNH VP7606, skull.

**Locality and Horizon**—Quebrada de La Mina, Potrerillos, Mendoza, Argentina. Cacheuta Formation, Late Triassic.

**Remarks**—This was the first described chigutisaurid.

**Taxonomic Position**—Chigutisauridae

*PELOROCEPHALUS TENAX*

*Chigutisaurus tenax* Rusconi 1949:93
*Pelorocephalus tenax* Marsicano 1999:figs. 7–9

**Material**—MCNA 2752 (holotype), skull with mandible articulated.

**Locality and Horizon**—Bajada de la Obligación, El Challao, Mendoza, Argentina. Río Blanco Formation, Late Triassic.

**Remarks**—The Chigutisauridae was formally erected by Rusconi (1949) in a brief description of *Chigutisaurus* (=*Pelorocephalus*) *tenax.* This single skull and mandible is the best preserved member of *Pelorocephalus* and the one from which our characters are taken.

**Taxonomic Position**—Chigutisauridae.

*PELOROCEPHALUS CACHEUTENSIS*

*Chigutisaurus cacheutensis* Rusconi 1953:1
*Pelorocephalus cacheutensis* Marsicano 1999:figs. 10–13

**Material**—MCNA 2966 (holotype), skull; MCNA 2968, mandible; PVL 3463, skull with mandible articulated and a humerus.

**Locality and Horizon**—Cerro Cacheuta, Cacheuta, Mendoza, Argentina. Cacheuta Formation, Late Triassic.

**Remarks**—PVL 3463 is the skull figured by Bonaparte (1978) associated with the postcranial skeleton of a smaller specimen.

**Taxonomic Position**—Chigutisauridae.

*PELOROCEPHALUS* SP.

PELOROCEPHALUS ISCHIGUALASTENSIS BONAPARTE 1975:538

**MATERIAL**—MCZ 4299 (HOLOTYPE), SKULL, MANDIBLES AND INTERCLAVICLE; UNCATALOGUED MCZ MATERIAL FROM THE TYPE LOCALITY.

**LOCALITY AND HORIZON**—SAN JUAN PROVINCE, ARGENTINA. ISCHIGUALASTO FORMATION, LATE TRIASSIC.

**REMARKS**—THIS MATERIAL IS INDETERMINABLE TO SPECIES THROUGH ITS POOR PRESERVATION.

**TAXONOMIC POSITION**—CHIGUTISAURIDAE.

*KERATOBRACHYOPS AUSTRALIS*

*Keratobrachyops australis* Warren 1981b:274, figs. 1–11

**Material**—QMF 10115 (holotype), skull and mandible; QMF 10116, part of a skull; QMF 10117, mandible; QMF 14488 skull and mandible; QMF 14487, partial skull.

**Locality and Horizon**—Queensland Museum field locality L215, Duckworth Creek, Bluff, Queensland, Australia. Arcadia Formation, Rewan Group, Early Triassic.

**Remarks**—A new more complete skull referrable to the same taxon was recently discovered and is not yet described, but was included in our analysis as *Keratobrachyops* sp.

**Taxonomic Position**—Basal Chigutisauridae.

*SIDEROPS KEHLI*

*Siderops kehli* Warren and Hutchinson 1983:5, figs. 1–23, 28–31, 33–34

**Material**—QMF 7882 (holotype), a nearly complete skull with postcranial skeleton in articulation.

**Locality and Horizon**—Kolane, Wandoan, Queensland, Australia. Westgrove Ironstone Member, Evergreen Formation, Early Jurassic.

**Remarks**—*Siderops* was the first undoubted post-Triassic temnospondyl described, and remains the most complete brachyopoid. Its assignment to the Chigutisauridae and the diagnosis of that taxon was based largely on brachyopoid plesiomorphies (Warren and Hutchinson, 1983). It is still true that the diagnosis of Chigutisauridae within Brachyopoidea is difficult. A substapedial ridge, as present in *Siderops,* has now been identified in all of the Argentinian chigutisaurids and remains a consistent synapomorphy for the taxon, in addition to the varied posterior projections from the skull which were not preserved in *Siderops.* In addition, the mandible of *Siderops* is extremely similar to those of the chigutisaurs *Compsocerops* and *Koolasuchus,* and in *Koolasuchus* a tabular horn is present on undescribed material. This association reaffirms the original assignation of *Siderops* to the Chigutisauridae.

**Taxonomic Position**—Chigutisauridae.

*COMPSOCEROPS COSGRIFFI*
(Fig. 3B)

*Compsocerops cosgriffi* Sengupta 1995:314, figs. 2–14

**Material**—ISI A 33 (holotype), a skull; ISI A 22, 24–27, 34–49, a left mandibular ramus and postcranial material including vertebrae and a clavicle.

**Locality and Horizon**—Near Rechni village, Pranhita-Godavari valley, Deccan, India. Maleri Formation, Late Triassic.

**Remarks**—This is the best preserved of the Indian chigutisaurids.

**Taxonomic Position**—Chigutisauridae.

### KUTTYCEPHALUS TRIANGULARIS

*Kuttycephalus triangularis* Sengupta 1995:325, figs. 15–18

**Material**—ISI A 50 (holotype), skull and left mandibular ramus; ISI A 51–52.

**Locality and Horizon**—Pranhita-Godavari valley, Deccan, India. Maleri Formation, Early Norian (Late Triassic).

**Remarks**—A lower jaw was mentioned as part of the holotype material (Sengupta, 1995) but it was neither described nor figured, thus it was not scored in the data matrix of the present analysis. Both of the Indian chigutisaurids share the exclusion of the maxilla from the naris and the presence of a posterior pterygoid projection with *Sinobrachyops*. *Kuttycephalus* has reduced interpterygoid vacuities.

**Taxonomic Position**—Chigutisauridae.

### KOOLASUCHUS CLEELANDI

*Koolasuchus cleelandi* Warren et al. 1997:4, figs. 2–6

**Material**—NMV P186213 (holotype), a mandible; NMV P156988, 186277, mandibular rami; NMV P186101, 186205, 186181, 186171, skull fragments; NMV P 186145, 186055, pterygoids; NMV P 186182, skull bone with orbit; NMV P186480, 186295, interclavicle; NMV P18237, 186144, 186155a, 186214, 186167, clavicles; NMV P186179, neural arch; NMV P186040, 186238, 186207,197908, 186142, 186253, 186354–5, centra; NMV P186481–2, 186155b, 186245, ribs; NMV P186158, cleithrum; NMV P186239, fibula.

**Locality and Horizon**—Southern coast of Victoria, Australia, between San Remo and Kilcunda. The locality of the holotype is Rowell's Beach. Early Cretaceous.

**Remarks**—*Koolasuchus* is known from four mandibular rami and a collection of postcranial material, none of which was articulated (Warren et al., 1997). A partial skull is not yet fully prepared but confirms the material has a tabular horn and pertains to the Chigutisauridae. This collection as yet includes insufficient cranial material to be included in the phylogenetic analysis but is scored in the matrix.

**Taxonomic Position**—Chigutisauridae.

### CHIGUTISAURIDAE indet.

Chigutisauridae Warren and Damiani (1999)

**Material**—BP/1/5252 (partial mandibular rami with fragments of skull), BP/1/4750 (fragmentary cranial and mandibular material).

**Locality and Horizon**—Lower Elliot Formation, Late Triassic

**Remarks**—These specimens were collected by Kitching and Raath (1984) and recorded as Capitosauridae. A re-examination of the material, which consists of fragments of the mandibular rami and skull roof, showed features not found in the Capitosauridae and characteristic of the Chigutisauridae (Warren and Damiani, 1999). The material was extremely similar to that from the Upper Elliot Formation (below). BP/1/4750 has an inner row of teeth on the palate which are larger than the maxillary row and an ectopterygoid tusk, neither of which are found in capitosaurids. A continuous palatal tooth row is characteristic of chigutisaurids rather than brachyopids.

**Taxonomic Position**—Chigutisauridae.

### CHIGUTISAURIDAE Warren and Damiani (1999)

**Material**—BP/1/5092 (partial skull and mandibular rami), BP/1/5111 (large fragments of skull and attached mandible, neural arches, centra, ribs, fragment of interclavicle), BP/1/5406 (fragments of skull, mandible, intercentrum, neural arch, femur).

**Locality and Horizon**—Upper Elliot Formation, Early Jurassic.

**Remarks**—Like that from the Lower Elliot Formation, this fragmentary material was also collected by Kitching and Raath (1984) but tabulated as Brachyopidae. Examination of the material (Warren and Damiani, 1999) shows it to be chigutisaurid. All of the specimens have a brachyopoid squamosal-quadratojugal trough. BP/1/5111 also has preserved the posterior end of the mandibular ramus, which is brachyopoid in that it is small and rounded in section, the angular extends a long way posteriorly beneath the ramus, the prearticular covers the posterodorsal face of the lingual surface so that the articular is not exposed lingually, but is chigutisaurid in the presence of a chordatympanic foramen. BP/1/5092 has broad, deeply impressed sensory canals between nostril and orbit (a brachyopoid character) a continuous inner row of teeth on the palate (a chigutisaurid character) and the teeth are keeled as they are in the Australian chigutisaurids *Siderops* and *Koolasuchus* and in the Argentinian chigutisaurid *Pelorocephalus cacheutensis*. The specimen was placed in *Siderops* by Warren and Damiani (1999) through the presence of a row of teeth on the posterior coronoid bone of the mandible. These are absent in other chigutisaurids.

**Taxonomic Position**—Chigutisauridae.

### BRACHYOPOIDEA indet.

*Austrobrachyops jenseni* Colbert and Cosgriff, 1974

**Material**—AMNH 9301 mandibular fragment.

**Locality and Horizon**—Coalsack Bluff, Transantarctic Mountains, Antarctica (AMNH 9346), Graphite Peak, Transantarctic Mountains, Antarctica (AMNH 9301). Lower Fremouw Formation, Early Triassic.

**Remarks**—AMNH 9301 is a temnospondyl mandibular fragment including part of the postglenoid area. Its postglenoid area is not traversed vertically by the mandibular sulcus of the sensory canal system so it is unlikely to be capitosauroid or rhytidosteid. The mandibular fragment is probably brachyopoid. The holotype of *Austrobrachyops jenseni* (AMNH 9342) was described as a brachyopid pterygoid (Colbert and Cosgriff, 1974). It is not demonstrably amphibian and most likely belongs to the dicynodonts. The name *Austrobrachyops jenseni* therefore becomes a nomen dubium.

**Taxonomic Position**—AMNH 9301 Brachyopoidea indet.

### BRACHYOPOIDEA incertae sedis.

*Austropelor wadleyi* Longman 1941:29, figs. 1–2

**Material**—QMF 2628 (holotype), mandibular fragment.

**Locality and Horizon**—Marburg Sandstone, Lowood, Queensland. Early Jurassic.

**Remarks**—This portion of mandible is important as the first-found post-Triassic temnospondyl, although it was originally thought to be reworked from the Triassic. Longman (1941) and Colbert (1967) described it as capitosaurid. It was thought to be closer to the brachyopoids than to the capitosaurs (Warren and Hutchinson, 1983).

**Taxonomic Position**—Brachyopoidea incertae sedis.

### HADROKKOSAURUS BRADYI (Welles 1947:246, figs. 3–6)

*Taphrognathus bradyi* Welles 1947:246, figs. 3–6
*Hadrokkosaurus* Welles 1957:982
*Hadrokkosaurus bradyi* Welles and Estes 1969:41, fig. 20

**Material**—UCMP 36199 (holotype), a mandibular ramus.

**Locality and Horizon**—Holbrook quarry, UCMP V 3922,

six miles west of Holbrook, Arizona, USA. Holbrook Member of the Moenkopi Formation, Early-Middle Triassic.

**Remarks**—The holotype of *H. bradyi* is a right mandibular ramus (UCMP 36199), the taxonomic affiliation of which is still not certain. It displays features not found elsewhere among stereospondyls (Jupp and Warren, 1986) such as a large foramen between the dentary and the surangular on the labial surface, a characteristic foramen in archosaurs. It does, however, have teeth which are labyrinthine in section. Welles (1947) originally referred this mandible and much of the postcranial material from the same locality to the Plagiosauridae. The jaw shares with the plagiosaurid *Plagiosternum* the position of the posterior meckelian foramen situated between the angular and prearticular.

**Taxonomic Position**—Brachyopoidea incertae sedis.

*FERGANOBATRACHUS RIABININI* Nessov, 1990:88, fig. 1

**Material**—TsNIGR 6/12217 (holotype), clavicle; TsNIGR 1–5/12217, centrum; TsNIGR 7–11/12217, cranial fragments; TsNIGR 12/12217, phalanx.
**Locality and Horizon**—Balabansay Formation, Tashkumyar, Kirgizia, Russia, Middle Jurassic.
**Remarks**—These fragmentary remains were described as Capitosauridae by Nessov (1990) but referred to the Brachyopidae by Shishkin (1991), apparently because of the similarity of one of the stereospondylous centra to *Gobiops desertus.*
**Taxonomic Position**—This material is not determinable within the Stereospondyli. As all known post-Triassic stereospondyls are brachyopoid we tentatively refer it to the Brachyopoidea incertae sedis.

BRACHYOPOID MORPHOLOGY

While the cranial morphology of both the Brachyopidae and Chigutisauridae have been known for some time and from several revisions, complete mandibles have been described only recently, and postcranial material of the Brachyopidae is rare and largely undescribed. This situation is true partly because, as with most early stereospondyl studies, descriptions have been centred around cranial material. For this reason we have provided a list of all known brachyopid and chigutisaurid postcranial material with a description of any new features and postcranial characters which are taxonomically useful. Cranial descriptions are restricted to new figures of *Brachyops laticeps,* the specimen on which the Brachyopidae was based (Fig. 2), and line drawings of some of the most complete brachyopid cranial material (Fig. 3). In these we indicate which parts of the skulls are actually present, unlike the idealised reconstructions of Welles and Estes (1969) in which missing or poorly preserved areas were restored (Welles and Estes, 1969:figs. 15–17). For instance, among brachyopids, the region between the orbit and naris is fully preserved only in *Xenobrachyops, Banksiops* and the enigmatic *Vigilius* and *Batrachosuchoides,* so character determination in that region is not possible in most taxa. Most of the original descriptions clearly indicate those areas of the skull which are actually present. We include also a drawing (Fig. 4) of the postglenoid area of the mandible of previously unfigured *Batrachosuchus* as well-preserved brachyopid mandibular material is rare, and reconstructions of brachyopoid dermal pectoral girdle elements (Figs. 5–6).

**Skull**

The original description of *Brachyops laticeps* (Owen, 1855) was accompanied by detailed drawings of the specimen in dorsal and left lateral view. These appear to have been accurate but some of the detail shown in them has been lost. Watson's (1956) redescription of the specimen was accompanied by line

drawings which corrected apparent parallax in the original drawings and contained detailed description of the state of preservation of the skull. Prior to its second redescription (Welles and Estes, 1969), the palate was prepared and the illustrations in that paper are the only ones of the palate and occiput. The specimen is poorly preserved in both areas and a third redescription is necessary to correct the stylised drawings of Welles and Estes.

On the skull roof (Fig. 2A) sutures are clearly visible in some areas. In other areas, where the ornament remains, they are indicated by interruptions to the pattern of ornament. Little bone is left in the antorbital region and no sutures are discernible so the presence or absence of a lacrimal, septomaxilla, lateral exposure of the palatine, and the sutural relations between the maxilla and these bones, cannot be determined. There is no evidence to indicate the position of the nares. It is clear that the postorbital does not suture with the parietal as it does in the Tupilakosauridae. The tabulars are well-preserved and do not bear horns or otic embayments; their suture with the postparietals cannot be determined.

Matrix remains around the margins of the palate obscuring the marginal teeth and most of the inner tooth row (Fig. 2B). Nevertheless tusks from the inner row are partially exposed as are two smaller teeth on the ectopterygoids and three probable teeth of the transvomerine row. All of the teeth are shorter than those shown by Welles and Estes (1969:fig. 15D). Anteriorly, in the region of the anterior palatal vacuity, no bone is preserved and the posterior margin of the vacuity is not visible. A suture between the vomer and the palatine is present on the left of the skull but no clear suture is preserved between the palatine and the ectopterygoid. While the area occupied by the exoccipitals is poorly preserved it is evident that they could not have sutured with either the pterygoids (laterally) or one another (medially) as figured (Welles and Estes, 1969:fig. 15B). The quadrates are missing.

In occipital view (Fig. 2C) no sutures are visible and the boundary between bone and matrix is indistinct. The skull has the characteristic inverted U-shaped brachyopoid palate with lateral squamosal-quadratojugal troughs. The region of the ascending ramus of the pterygoid is not prepared so that the presence of an upper palatoquadrate fissure cannot be determined. Hence little of the detail shown by Welles and Estes (1969:fig. 15C) is visible, their reconstruction having been extrapolated from other brachyopids, presumably the isolated pterygoids from the Moenkopi Formation.

**Mandible**

Since a complete brachyopid mandibular ramus has been described in an Australian specimen (Damiani and Warren, 1996), complete rami are known in several chigutisaurids (Warren, 1981a; Warren and Hutchinson, 1983; Sengupta, 1995; Marsicano, 1993a; Damiani and Warren, 1996; Warren et al., 1997), and the differences in the arrangement of the bones on the postglenoid area has been figured (Warren et al., 1997), it is unnecessary to refigure these elements. The previously undescribed postglenoid area (PGA) of another specimen of *Batrachosuchus* sp. (UCMP 140591) is figured (Fig. 4) to illustrate the extreme elongation of the PGA in typical brachyopids. Although the posterior end of this PGA is still incomplete, it is longer than those *Batrachosuchus* mandibles figured previously (Watson, 1956; Colbert and Cosgriff, 1974). In UCMP 140591, UCMP 140590 and also in UCMP 48256 (Colbert and Cosgriff, 1974) the prearticular meets the surangular on the dorsolingual surface of the PGA, a bone arrangement synapomorphic for chigutisaurids. The former two specimens appear to be laterally compressed, perhaps because the articular is poorly ossified between the surangular and prearticular and the situation may be
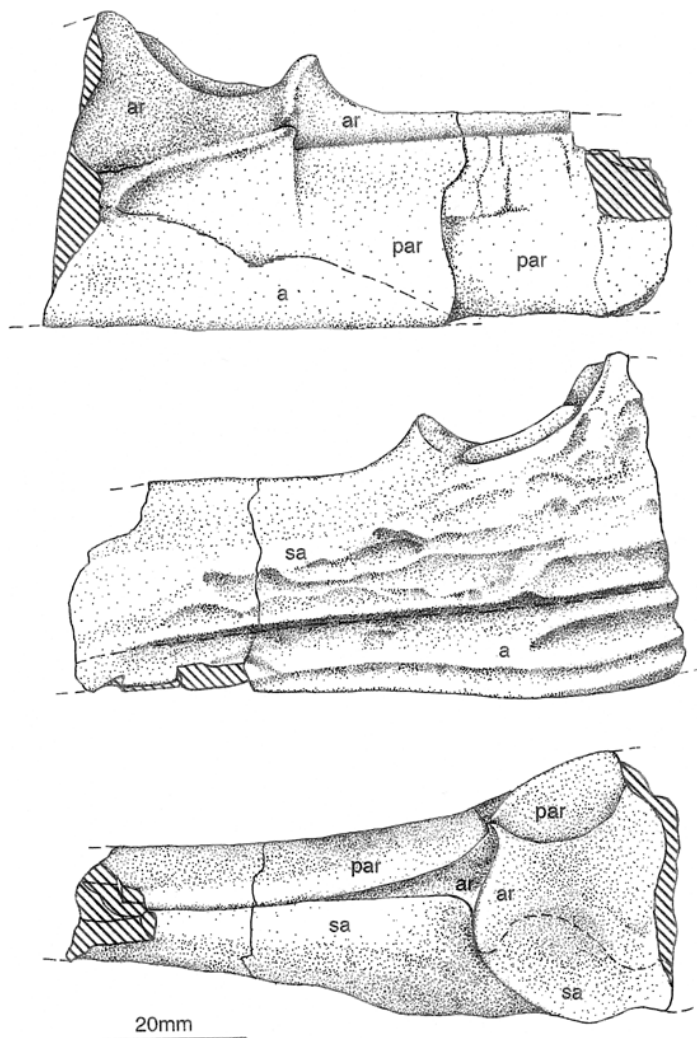
FIGURE 4.    Postglenoid area (PGA) of the right mandibular ramus of a member of the Brachyopidae, *Batrachosuchus* sp., UCMP 140591. Top, lingual (anterior to the left); middle, labial; and bottom, dorsal views. Note the surangular and prearticular clasp the lingual and labial sides of the PGA. In Brachyopidae they are normally separated dorsally by a tongue of articular, whereas in Chigutisauridae they often suture dorsally, while a little of the articular may be exposed on the lingual side of the PGA (the primitive condition). The chordatympanic foramen is absent in Brachyopidae. Cross-hatching represents broken bone. **Abbreviations**: **a**, angular: **ar**, articular; **par**, prearticular; **sa**, surangular.

similar in UCMP 48256. In the data matrix we have chosen to score the prearticular as separated from the surangular by a tongue of the articular, the condition shown in a fourth specimen of *Batrachosuchus* sp., UMZC T194 (Watson, 1956). The fact that the two bones almost always meet in the Chigutisauridae, in which the replacement bones are better ossified than in brachyopids, and do not meet in the better ossified brachyopids (especially *Xenobrachyops,* Warren, 1981a) suggests that their apparent junction in the three specimens of *Batrachosuchus* (above) is an artifact of preservation.

**Postcranial Skeleton**

Postcranial material has rarely been described associated with members of the Brachyopidae. In contrast, the chigutisaur, *Siderops,* was preserved with an almost intact postcranial skeleton. Postcranial material of apparent brachyopid nature has been recovered from the Moenkopi Formation and can perhaps be associated with *Vigilius,* from the Karoo where it has been described as *Batachosuchus browni,* the N'taweri Formation (*B. concordi*), and from the Knocklofty Formation of Tasmania

(*Blinasaurus = Banksiops*). The probable juvenile brachyopid, *Platycepsion wilkinsoni,* is associated with articulated postcranial material, but is poorly preserved. Some postcranial material is associated with all known chigutisaurs, although it has not been found in articulation other than in *Siderops.* Using the above material we were able to describe some of the postcranial skeleton of the brachyopoids and derive some diagnostic characters from it.

**Centra**—The centrum of the atlas of the Brachyopidae is known from seven specimens. An atlas was attached to the condyles of *Brachyops laticeps* (Owen, 1855) but is not with the specimen loan and remains undescribed. These elements were initially described for *Batrachosuchus* sp. (Watson, 1956) and later for *Batrachosuchoides* (Shishkin, 1966), *Batrachosuchus* sp. and *Hadrokkosaurus* (=*Vigilius*) (Welles and Estes, 1969), *Banksiops townrowi* (Cosgriff, 1974) and *Batrachosuchus concordi* (Chernin, 1977). Shishkin (1991), describing the atlas of *Gobiops,* noted that the atlas of brachyopids had a broad, 'low' centrum which 'narrowed rearward.' This breadth of the atlas is reflected in the large size of the exoccipital con-

and characterised by neural spines which are tall for stereospondyls, an exception being the arch associated with *Koolasuchus* (Warren et al., 1997). In *Siderops* (Warren and Hutchinson, 1983) the spines are almost square in section, but are more slender in *Pelorocephalus* (Marsicano, 1993b). A small, poorly-preserved ?caudal neural arch (UCMP 140580) collected with material attributed to *Batrachosuchus* sp. is identifiable only as stereospondyl.

**Haemal Arch**—This element is known only in *Siderops* (Warren and Hutchinson, 1983). So few stereospondyl haemal arches are known that comparisons are not meaningful.

**Ribs**—An almost complete series of articulated ribs were present in *Siderops* (Warren and Hutchinson, 1983). Overall they are more slender than in most stereospondyls, are less expanded distally and, in the pectoral area, have smaller uncinate processes. Similar ribs were described in *Pelorocephalus* (Marsicano, 1993b).

**Interclavicle (Fig. 5)**—In the chigutisaurids *Siderops* (Warren and Hutchinson, 1983), *Pelorocephalus* (Marsicano, 1993b) and *Koolasuchus* (Warren et al., 1997), the interclavicle is kite-shaped (deloid) and a little longer than wide, with a squared off parasternal process with unornamented margins. A fragmentary interclavicle of *Compsocerops* is incomplete on most borders.

An interclavicle of a similar shape to the interclavicle in the chigutisaurids was preserved in the brachyopid *Platycepsion* (Warren and Marsicano, 1998). More anteroposteriorly elongate interclavicles were described associated with brachyopid material in Tasmania (Cosgriff, 1974). Undescribed interclavicular material of *Batrachosuchus* sp. (UCMP 140584) and *Xenobrachyops* (QMF39651) is too incomplete for comparison with chigutisaurids.

**Clavicle (Fig. 6)**—Clavicles associated with the chigutisaurids *Siderops* (Warren and Hutchinson, 1983), *Pelorocephalus* (Marsicano, 1993b), *Compsocerops* (Sengupta, 1995), and *Koolasuchus* (Warren et al., 1997) are remarkably well preserved and similar in shape. A small, subtriangular blade curves abruptly dorsally at its posterolateral corner to form a slim, unflanged, rod-like dorsal (ascending) process which does not incline more than slightly posteriorly until near its distal end. At this point it is also inclined laterally. A section through the upper third of the process shows a convexity in the posterior border for articulation with the cleithrum. No flange is present on the anterior border of the dorsal process or along the posterolateral border of the clavicular blade. In *Koolasuchus, Compsocerops* and *Siderops,* and probably all chigutisaurids, the clavicular blade is indented on the medial margin.

Among brachyopids no complete clavicular remains have been found. Partial clavicles of *Blinasaurus henwoodi* (Cosgriff, 1969), *Gobiops desertus* (Shishkin, 1991), *Ferganobatrachus riabinini* (Nessov, 1990), *Vigilius wellesi* (referred to the Plagiosauridae, Welles, 1947), *Blinasaurus townrowi* (Cosgriff, 1974) and *Platycepsion wilkinsoni* (Warren and Marsicano, 1998) are described. A partial clavicle, QMF 39652, associated with the mandible of *Xenobrachyops* may be brachyopid. Although a complete dorsal process is present only in *B. wilkinsoni,* sections of the base of the process are present in some cases. Using all available material including undescribed clavicles of *Batrachosuchus* sp. Cosgriff (1974) described the brachyopid dorsal (cleithral) process as rod-like with a distinct posterior slope so that the distal end of the process would have terminated well posterior to the clavicular blade. The process lacks a flange on its anterolateral margin. All the known clavicular material appears to conform to this morphology although in none is the dorsal process complete. This rod-like process is similar to the dorsal process in the Chigutisauridae but in that taxon the process arises almost vertically and slopes a little posteriorly towards its distal end. An exception to this
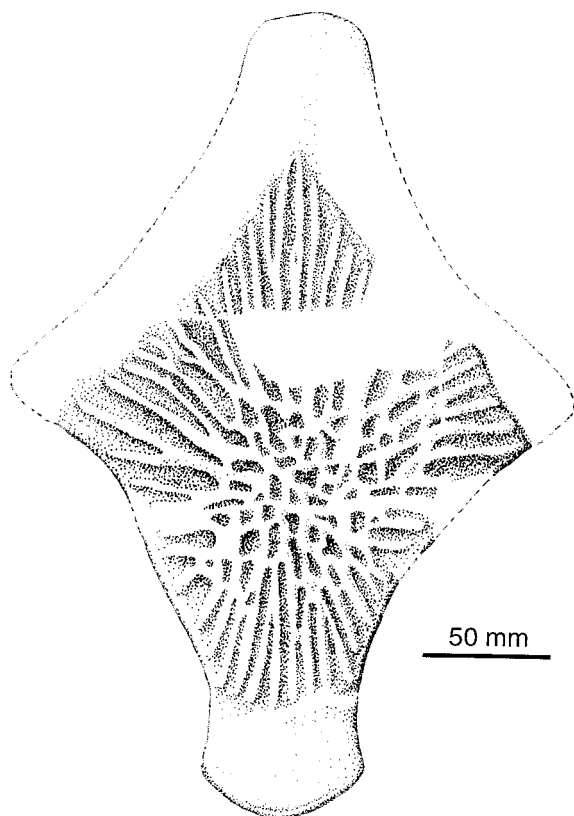


FIGURE 5. Interclavicle of *Siderops* to show the truncated parasternal process (redrawn from Warren and Hutchinson, 1983).

dyles in brachyopids. Brachyopid atlantes are also anteroposteriorly elongate. In chigutisaurs the two known atlantes (*Siderops* and *Pelorocephalus*) are elongate but not so dorso-ventrally compressed as in the brachyopids. The atlas of brachyopoids is thus more anteroposteriorly elongate than it is in stereospondyls other than plagiosaurs.

Brachyopid axes are stereospondylous, the single exception being the crescentic axis described in *Batrachosuchoides* (Shishkin, 1966). Stereospondylous axes are described for *Batrachosuchus* sp. (Welles and Estes, 1969), *Gobiops* (Shishkin, 1991), and *Batrachosuchus concordi* (Chernin, 1977). In the only known chigutisaurid axis, that of *Siderops,* the notochordal canal is open dorsally (Warren and Hutchinson, 1983). This axis, and that of *Batrachosuchoides,* thus closely resemble rhachitomous intercentra except that they are opisthocoelous and may have lacked a neural arch.

Other centra in the Brachyopidae and Chigutisauridae are rhachitomous apart from post-Triassic members in which there is sometimes a tendency to stereospondylous centra. These are found together with rhachitomous (crescentic) intercentra in *Gobiops* (Shishkin, 1991), *Koolasuchus* (Warren et al., 1997), and in the Elliot Formation of South Africa (Warren and Damiani, 1999) but in *Siderops* (Warren and Hutchinson, 1983) all centra posterior to the atlas are crescentic, and stereospondylous centra are unknown in the Argentinian (Bonaparte, 1978; Marsicano, 1993b) and Indian (Sengupta, 1995) chigutisaurs.

Within brachyopoids, a single ossified pleurocentrum is associated with *Batrachosuchus* sp. material (UCMP 42856) but many pleurocentra are preserved in *Pelorocephalus* (Marsicano, 1993b), and pleurocentra were fused to the intercentrum in one vertebra of *Compsocerops* (Sengupta, 1995).

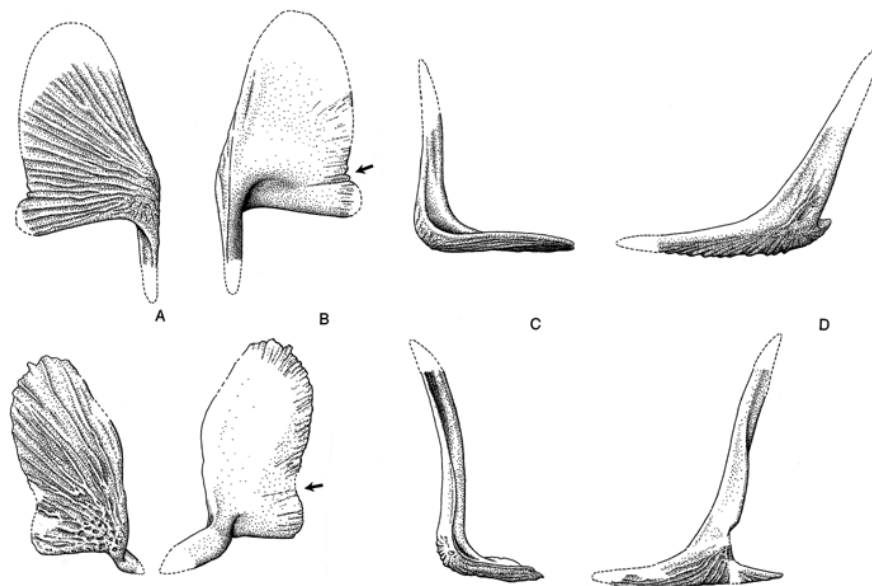**Neural Arch**—Chigutisaurid neural arches are well ossified

FIGURE 6.   Clavicles of Brachyopoidea. Upper row, reconstructed clavicles of Brachyopidae, based on *Batrachosuchus* (UCMP 140583, UCMP 140573 and UCMP 140570); lower row, reconstructed clavicles of Chigutisauridae, based on *Compsocerops* (redrawn from Sengupta, 1995) (A, B, C) and *Siderops* (redrawn from Warren and Hutchinson, 1983) (D). **A**, ventral; **B**, dorsal; **C**, posterior; and **D**, lateral views. Note the greater posterior slope of the dorsal process of the clavicle in Brachyopidae and the indentation in the clavicular blade. Not to scale.

structure was described in the Jurassic *Gobiops* in which the dorsal process was described as ornamented, triangular and very low, comparable with the process in *Tupilakosaurus* (Shishkin, 1991). We have reconstructed the brachyopid clavicle (Fig. 5) from the *Batrachosuchus* material (UCMP 140570, 140573 and 140583) in which the dorsal process is fairly well preserved. In UCMP 140570 the clavicular blade is small and indented as in chigutisaurids suggesting that this may be common to all brachyopoids. The indentation occurs elsewhere in temnospondyls, for example in plagiosaurs.

**Other Pectoral Girdle Elements**—Cleithra are known in *Siderops* (Warren and Hutchinson, 1983) and *Koolasuchus* (Warren et al., 1997), while scapulocoracoids in which the supraglenoid foramen is open were present in *Siderops* and *Pelorocephalus* (Marsicano, 1993b).

**Forelimb Bones**—Humeri have been described for *Vigilius wellesi* (Welles and Estes, 1969), *Batrachosuchus* sp. (Welles and Estes, 1969), *Siderops* (Warren and Hutchinson, 1983), *Pelorocephalus* (Marsicano, 1993b) and *Compsocerops* (Sengupta, 1995). All of these are typical of stereospondyl humeri although those of the brachyopids are a little better ossified with well-developed supinator processes. In *Gobiops* the humerus differs in that the degree of torsion between the distal and proximal ends is reduced (Shishkin, 1991). A radius was described in *Pelorocephalus* (Marsicano, 1993b). Other distal forelimb bones are unknown in brachyopoids.

**Ilium and Ischium**—A small piece of distal ilium (UCMP 140579) was associated with *Batrachosuchus* sp. Material associated with *Composcerops* (Sengupta, 1995) included an ilium which resembles that of *Siderops* (Warren and Hutchinson, 1983) and most stereospondyls in being flared dorsally. In contrast, the ilium of *Pelorocephalus* (Marsicano, 1993b) is more elongate and does not flare dorsally, similar to the condition in metoposaurs (Warren and Snell, 1991). Poorly preserved ischia were present in *Siderops* (Warren and Hutchinson, 1983) and *Pelorocephalus* (Marsicano, 1993b).

**Hind Limb Bones**—An unremarkable brachyopid femur was described for *Banksiops townrowi* (Cosgriff, 1974). Within chigutisaurids a slender partial femur was preserved in *Siderops*

(Warren and Hutchinson, 1983) and a similar, almost complete element in *Pelorocephalus* (Marsicano, 1993b). Characteristic temnospondyl tibia and fibula were described for *Pelorocephalus* (Marsicano, 1993b) and an isolated fibula for *Koolasuchus* (Warren et al., 1997).

**Postcranial Apomorphies**

While much of the brachyopoid postcranial skeleton differs little from that of most other stereospondyls, some morphological features are characteristic of brachyopoids as a whole. These are the elongate atlas, the shape of the dorsal process of clavicle, and the narrow pectoral girdle. The interclavicular shape with a posteriorly squared-off parasternal process may be characteristic of chigutisaurids.

The massive, posteriorly narrowing, elongate atlas was first pointed out by Shishkin (1966) who likened the brachyopid atlas to those of Metoposauridae and Plagiosauridae and contrasted them with the higher, shorter, and less massive atlantes of capitosaurs. The brachyopoid atlantes described above agree with Shishkin's description. They are longer than those of metoposaurids but not as elongate as in plagiosaurs. Within the context of the present analysis the elongate atlas of brachyopoids is derived.

The unexpanded, rod-like dorsal process of the clavicle is undoubtedly a synapomorphy of the Brachyopoidea. In the Brachyopidae it appears to slope sharply posteriorly from the base to terminate behind the ventral clavicular blade, while in the Chigutisauridae it extends vertically above the posterior border of the blade before sloping a little towards the tip. The chigutisaurid dorsal process is paralleled by the condition in *Dvinasaurus* but is unlike that in the Tupilakosauridae which have a low process which is transversely elongate (Warren, 1999).

In the three chigutisaurids in which the posterior process of the interclavicle is known (*Siderops, Koolasuchus, Pelorocephalus*), it is truncated rather than pointed and its margins are unornamented.

It was suggested (Warren and Marsicano, 1998) that the com-

bined width of the pectoral girdle in brachyopoids was considerably narrower than the skull width, and that this condition might be a synapomorphy of brachyopoids. The condition was first reported in *Siderops kehli* (Warren and Hutchinson, 1983) and is also present in *Platycepsion wilkinsoni* (Warren and Marsicano, 1998). The only other articulated brachyopoid, the chigutisaur *Pelorocephalus* (Bonaparte, 1978) was not found in articulation and was constructed from dispersed elements. The pectoral girdle appears to have been widened artificially and in reality was much narrower. In the Tupilakosauridae, the only articulated material of the pectoral girdle is found in three specimens of the southern African *Thabanchuia oomie* (Warren, 1999) and in *Kourerpeton bradyi* (Olson and Lammers, 1976). In all four the girdle is the same width as the skull.

### PHYLOGENETIC ANALYSIS

A recent phylogeny of the higher temnospondyls confirmed a brachyopoid clade, consisting of *Keratobrachyops* as the sister-taxon of the Brachyopidae + Chigutisauridae, nested within the stereospondyl clade (Yates and Warren, 1999). This PAUP analysis contradicted earlier manually produced cladograms in which the brachyopids were placed in a clade outside the Stereospondyli with the Russian *Dvinosaurus* and *Tupilakosaurus* (Coldiron, 1978; Milner, 1990). A previous PAUP-based study of the brachyopoids (Damiani and Warren, 1996) confirmed a sister-group relationship between the brachyopids and chigutisaurids and placed the entire brachyopoid taxon as sister group to *Tupilakosaurus* outside the stereospondyl clade. This conclusion was correct given the limited outgroups used and clearly illustrates one of the problems of cladistics; that the 'correct' answer relies on an analysis of the maximum available data from the total known taxa, a methodology which is not practicable.

### Material and Methods

The phylogenetic analysis presented here was based on 60 characters (58 cranial and 2 postcranial) (Appendix 1) for seventeen brachyopoid ingroup taxa and five outgroups (Appendix 2). The outgroups used to determine character polarity were selected according to previous phylogenetic analyses (Damiani and Warren, 1996; Yates and Warren, 1999) and also the analysis of Milner (1990). The brachyopoid taxa *Notobrachyops, Batrachosuchoides* and *Koolasuchus,* although scored in the data matrix (Appendix 2), were excluded from the analysis as they are represented by incomplete specimens. Including them greatly increased the instability of the resultant cladogram and thus the number of equally parsimonious trees, and their status is discussed separately. The brachyopids *Batrachosuchus concordi* and *Platycepsion wilkinsoni* were excluded from the analysis as we considered them to be immature individuals, and therefore not adequate for phylogenetic inferences to be made (Hennig, 1966; Chiappe et al., 1996). In the present analysis there are obvious differences in proportions between immature and mature taxa as well as differences in the degree of ossification both of which could affect character distribution. The specimens are scored in the data matrix.

All characters were treated as unordered and unweighted, with the exception of characters 26 and 53 which were considered as ordered. The characters and character state distribution are listed in Appendix 1. The matrix was executed using the heuristic Stepwise Addition algorithm in PAUP (Phylogenetic Analysis Using Parsimony version 3.1.1; Swofford, 1993).

### Results and Discussion

Twelve equally parsimonious trees of 149 steps (CI: 0.60; RI: 0.76) were generated by the program and the 50% Majority-rule consensus tree is presented in Figure 7.
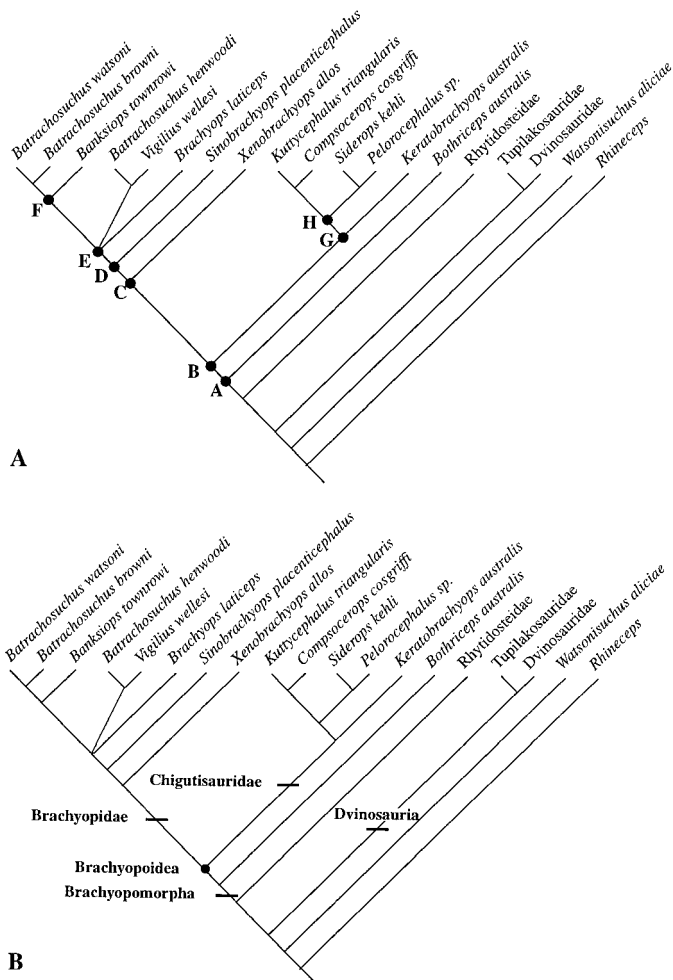


FIGURE 7. Brachyopoid phylogeny resulting from the present analysis (50% Majority Rule). **A**, clades represented by nodes A–H are discussed in the text; **B**, showing the principal node and stem based higher taxa considered.

The monophyly of the Brachyopomorpha taxon nov. (node A, Fig. 7) is supported by several unique synapomorphies as follows: deeply incised sensory sulci between nostrils and orbits (4. 2); rounded stalked exoccipital condyles (38); ascending ramus of the pterygoid arises from the dorsal surface of the pterygoid as a gently concave lamina (46. 3); coronoid dentition restricted to the middle and/or posterior coronoids (57. 1); PGA of the mandible slender and elongated (52. 2); and dorsal process of the clavicle without anterior flange (59. 1). Four more derived conditions for this group are homoplastic: inverted U-shaped palate (21); the presence of the prearticular on the lingual surface of the PGA (53. 2); quadrate condyles with two parts subequal in size (24. 2); and absence of mandibular sulcus of the sensory canal system (51). This situation is due to the presence in the clade (*Dvinosaurus* + Tupilakosauridae) of an inverted U-shaped palate and quadrate condyles with two parts subequal in size, and the reversal of characters 53 and 51 in *Keratobrachyops.*

Within the Brachyopomorpha, two monophyletic groups are clearly defined, the Brachyopidae and Chigutisauridae, with the Australian taxon *Bothriceps* as the sister-taxon of both. This basal position of *Bothriceps* is probably related to the presence in the specimen of a number of primitive characters which, combined with the lack of information about 30% of the char-

acters in the only specimen known, resulted in its placement as a stem brachyopoid. Some of these plesiomorphies are: the presence of a pterygoid flange (19), the absence of a contact between the exoccipitals and the pterygoid on the palate (18), and the presence of ornament on the pterygoids (27). It is likely that *Bothriceps* possessed a tabular horn which supports its position as a basal brachyopoid.

The clade Brachyopoidea (node B, Fig. 7) is justified by the following homoplastic characters: deeply incised sensory sulci between nostrils and orbits only (4. 2), reversed in *Vigilius*; cultriform process of the parasphenoid narrow and flat (28. 1), reversed in *Siderops*; and in the mandible the articular is excluded from the lingual wall of the PGA by a posterior growth of the prearticular (53), reversed in *Keratobrachyops*.

The clade Brachyopidae (node C, Fig. 7) is united by six synapomorphies: reduced tooth row on palatines and ectopterygoids (32. 1); absence of a column on the ascending ramus of the pterygoid (47); the rod-like dorsal process of the clavicle slopes posteriorly from its base (59. 2); and the postglenoid area in the mandible is very elongate, slender (52. 3) and lacks a chordatympanic foramen (50. 2). The other derived conditions for this clade that appear as homoplastic are: articular below the level of the dentary tooth row (54); also present in *Keratobrachyops*; prearticular process of the mandible absent (56), as in some of the outgroups; the absence of an otic notch (11) and of tabular horns (12) also occur in the clade (*Dvinosaurus* + Tupilakosauridae); posttemporal fenestra as wide as deep (41) (reversed in *Banksiops*); maximum width of the interpterygoid vacuity pair greater than 90% of their length (34), present also in Rhytidosteidae.

The monophyletic group (*Sinobrachyops* + ((*Vigilius* + *B. henwoodi*) + *Brachyops* + (*Banksiops* + (*B. browni* + *B. watsoni*)))) (node D, Fig. 7) is supported by two unique synapomorphies: presence of an upper (37) palatoquadrate fissure and an enlarged foramen in the lateral wall of the exoccipital (40). Other derived conditions of this clade appear as homoplastic: nares very close to the midline (8) which reverses in *Vigilius*; pterygoid-exoccipital suture present (18) as it is in Tupilakosauridae and Chigutisauridae; subtemporal vacuity extends anteriorly further than the midpoint of the interpterygoid vacuity (35), a condition also present in the chigutisaurid *Compsocerops*; presence of a lower palatoquadrate fissure (36), also present in *Bothriceps,* and posteriorly projected exoccipital condyles (48), a condition also known in the Indian chigutisaurids and in (*Dvinosaurus* + Tupilakosauridae).

The clade (*Brachyops* + (*Vigilius* + *B. henwoodi*) + (*Banksiops* + (*B. browni* + *B. watsoni*))) (node E, Fig. 7) is justified by three synapomorphies: absence of a lateral exposure of the palatine (10), also absent in the outgroups; narrow subtemporal vacuity (20), present also in *Dvinosaurus* + Tupilakosauridae, and absence of a paraquadrate foramen (42. 2), an absence shared with *Bothriceps* and the Indian chigutisaurid *Kuttycephalus*. Within this monophyletic group the relationships among the clades (*Vigilius* + *B. henwoodi*), (*Banksiops* + (*B. browni* + *B. watsoni*)) and *Brachyops* remains unresolved.

The sister-taxon relationship between *Vigilius* + *B. henwoodi* is supported by only one synapomorphy, the presence of enlarged orbits (3).

Within node E, the clade (*Banksiops* + (*B. browni* + *B. watsoni*)) (node F, Fig. 7) is justified by three synapomorphies: the absence of a tooth row on the palatines and ectopterygoids (32. 2); the presence of ornament on the parasphenoid and/or pterygoid (27), which is also present in some of the outgroups, in *Bothriceps* and *Keratobrachyops,* and in other more basal stereospondyls; and the presence of a broad and flat cultriform process (28. 2), which is also present in the Indian *Kuttycephalus* and in the Rhytidosteidae. The sister-taxon relationship between the South African *Batrachosuchus* taxa is supported

by the autapomorphic presence of a flange on the occipital portion of the squamosal (49) and the homoplastic character, a slightly developed prearticular process on the mandible (56. 1), as is found also in chigutisaurids.

The monophyly of the Chigutisauridae is supported by two unique synapomorphies (node G, Fig. 7): the presence of a substapedial ridge (45), and an ascending ramus of the pterygoid which is gently concave and posteriorly recurved in vertical section (46.4). Other derived conditions for this group are homoplastic as they are also present in some of the outgroups: the width of the interpterygoid vacuity pair less than 90% of their length (34), and the posterior meckelian foramen bordered by the prearticular and postsplenial (55. 1).

Within Chigutisauridae, the basal position of *Keratobrachyops,* as the sister-taxon of all remaining chigutisaurids, is the result of the presence in that taxon of several primitive conditions for the clade as follows: the lack of skull table projections, the presence of a pterygoid flange, the absence of a contact between exoccipitals and pterygoids on the palate, and the presence of a mandibular sulcus on the postglenoid area of the mandible. The first three characters are shared with *Bothriceps*.

The clade ((*Pelorocephalus* + *Siderops*) + (*Compsocerops* + *Kuttycephalus*)) (node H, Fig. 7), is justified by the presence of postsquamosal (14) and postquadratojugal processes (15) on the skull roof.

The sister-group relationship between the *Pelorocephalus* taxa and *Siderops* is justified by the presence of a suture between the surangular and prearticular on the PGA (53. 3). The Indian *Compsocerops* and *Kuttycephalus* are sister taxa supported by five synapomorphies: jugal extends well anterior to the orbit (5), the maxilla is excluded from the border of the naris (9), the presence of a postparietal process (16), the absence of denticles on the coronoids (57. 2), and the posterior process on the medial part of the quadrate ramus of the pterygoid (23), although this last condition is also present in the brachyopid *Sinobrachyops*.

The phylogenetic analysis presented here supports the monophyly of Brachyopoidea and of the two clades within it, the Brachyopidae and Chigutisauridae. Although homoplastic with the Brachyopoidea in many features, *Dvinosaurus* and the *Tupilakosauridae* are clearly related to one another and to other more basal temnospondyls outside the Stereospondyli as was hypothesised by Yates and Warren (2000). In the analysis, *Bothriceps* falls outside the definition of Brachyopoidea (Yates and Warren, 2000) as a result of the presence of many plesiomorphies in that taxon. Many characters could not be scored for *Bothriceps* and a more complete specimen could well show its relationship as closer to the basal chigutisaur, *Keratobrachyops*. For this reason and to attempt to preserve the stability of phylogenetic taxa we have erected the stem based taxon Brachyopomorpha (node A, Fig. 7) to include stem brachyopoids.

Within the Brachyopidae, the Australian *Xenobrachyops* and the Chinese *Sinobrachyops* appear as successive sister taxa of an unresolved clade which includes all the 'true' brachyopids, that is, the ones stereotyped by Welles and Estes (1969). With the exception of *Vigilius,* these taxa are all extremely similar morphologically. Several of them are poorly preserved and all of them are represented by a single incomplete skull as is the case with most taxa in our analysis. We consider the genera *Batrachosuchus* (*B. browni* and *B. watsoni*) and *Banksiops* to be distinct as both are distinguished by autapomorphies. *Batrachosuchus henwoodi* was placed in *Batrachosuchus* (Warren and Marsicano, 1998) as it was clearly distinct from *Xenobrachyops* and *Banksiops,* the other Australian genera, and *Batrachosuchus* is the most clearly-defined of the central brachyopids. Moreover, *B. henwoodi* could not be distinguished from the other species of *Batrachosuchus* except for its enlarged orbits, which is the single character it shares with *Vigilius*. The

specimen of *Brachyops,* although the first-described taxon and represented by an almost complete skull, is preserved in such a way that insufficient characters are available to define the genus. Failure to distinguish between the branches of this trichotomy within the Brachyopidae is thus a combination of poor preservation, the resultant lack of clear character definition and also the absence of informative characters in the taxa concerned. As discussed above, we consider the position of *Vigilius* uncertain within the ingroup as many of the autapomorphies of that taxon strongly suggest affinity with the Dvinosauria.

In the our analysis, *Keratobrachyops* appears as the most plesiomorphic member of the Chigutisauridae in 8 of the 12 most parsimonious trees while in 4 of the trees it appears as a basal brachyopid. Among the remaining chigutisaurids the position of *Siderops* appears equivocal, as the sister taxon to the Argentinian *Pelorocephalus* species in 8 of 12 trees and as a stem taxon to Indian and Argentinian genera in the remaining 4 trees. This situation is a result of the lack of information, in *Siderops,* about the posterior skull projections present in all other chigutisaurids except *Keratobrachyops.*

In conclusion, it is of interest that the most plesiomorphic members of the Brachyopidae (*Xenobrachyops*) and Chigutisauridae (*Keratobrachyops*) are from Australia and the sister taxon to the Brachyopoidea (*Bothriceps*) may be Australian also. This presence in the earliest Triassic of Australia of all plesiomorphic members of the Brachyopoidea lends support to previous hypotheses that the stereospondyls originated and radiated in Gondwana (Milner, 1990) or East Gondwana (Yates and Warren, 2000; Warren et al., in press).

## ACKNOWLEDGMENTS

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## APPENDIX 1

### Characters and Character States Used in the Brachyopoid Phylogenetic Analysis

1. Skull elongate (0); skull shortened, as wide as long or wider than long (1).

In Rhytidosteidae some skulls are straight-sided as are the skulls of Lydekkerinidae, but some are parabolic. Hence the term parabolic as it is usually applied to brachyopoids is inappropriate in this data matrix. All of these taxa share the shortened skull although they are not necessarily closely related. This character applies in adult individuals only.

2. Orbits located posterior to the skull midlength (0); orbits located about half way along skull midline (1); orbits located anterior to the skull midlength (2).

3. Orbits not enlarged in the adult (maximum width of skull more than 7 times maximum width of orbit) (0); orbits enlarged (maximum width of skull less than 6.5 times maximum width of orbit) (1).

4. Sensory sulci well developed (0); present but poorly developed (1); deeply incised between orbit and nostril only (2); sensory sulci absent (3).

5. Jugal extends well anterior to orbit (0); anterior end of jugal about level with or posterior to anterior orbital margin (1).

6. Lacrimal bone present on skull roof (0); absent (1).

7. Maxilla and nasal not in contact (0); maxilla and nasal forming a suture (1).

8. Nares not close to skull midline (distance between nares twice width of one naris, or greater) (0); nares close to skull midline (distance between nares approximates width of one naris) (1).

9. Maxilla enters narial border (0); maxilla excluded from narial border by premaxilla-nasal suture (1).

10. Lateral exposure of the palatine (LEP) absent (0); reduced and unornamented, barely exposed on skull roof (1); well exposed on skull roof and ornamented (2).

A small slip of the palatine bone is present on the inner wall of the lateral margin of the orbit in *Xenobrachyops* and *Sinobrachyops*. It is difficult to detect and the character cannot be checked in most material because of poor or incomplete preservation. On the other hand, the LEP of *Batrachosuchoides* is easily detected as it is in Dvinosauria.

11. Otic notch present (0); reduced to otic embayment (1); otic notch absent (2).

12. Tabular horns present, robust, supported from below by an extension of the paroccipital process(0); reduced and unsupported distally (1); tabular horn absent (2).

13. Tabular horn with posteroventral extension (0); posteroventral extension absent (1).

A marked extension of the dorsal part of the paroccipital process is present immediately below and posterior to the tabular horn of the skull roof in Archegosauridae and Rhinesuchidae.

14. Post squamosal process of the skull roof, absent (0); present (1).

15. Post quadratojugal process of the skull roof, absent (0); present (1).

16. Post postparietal process of the skull roof, absent (0); present (1).

17. Dorsomedial process of the body of the pterygoid abuts the parasphenoid (0); the pterygoid forms a longitudinal contact or suture with the lateral margins of the parasphenoid plate in the adult (1).

18. Pterygoid separated from exoccipital by the parasphenoid (0); pterygoid-exoccipital suture present (1).

19. Palatine ramus of the pterygoid bears a posterolateral flange which projects into the subtemporal vacuity (0); flange absent (1).

20. Lateral border of the pterygoid beside the subtemporal vacuity concave so that the subtemporal vacuity is wide (0); lateral border of the pterygoid parallel to skull midline resulting in a narrow subtemporal vacuity (1).

21. Quadrate ramus of the pterygoid level with palate (0); sharply downturned (inverted U-shaped palate) (1).

22. Palatine ramus of the pterygoid reaches the vomer (0); palatine ramus of the pterygoid retracted posteriorly so that the palatine is exposed in the interpterygoid vacuity (1).

23. Posterior process on the margin of the medial part of the quadrate ramus of the pterygoid, absent (0); present (1).

24. Quadrate condyle double and markedly screw-shaped with the medial condyle extended anteriorly (0); quadrate condyle double and triangular, the apex of the triangle lateral (1); quadrate condyle double with the two parts subequal in size (2).

A triangular quadrate is characteristic of Rhytidosteidae and *Lydekkerina* whereas in brachyopoids the condyle has two subequal parts with the medial part slightly larger in Chigutisauridae.

25. Basioccipital ossified so that it contributes to occipital condyle (0); not ossified (1).

26. Pterygoid meets palatine on the lateral margin of interpterygoid vacuity (0); pterygoid retracted so ectopterygoid is exposed in the interpterygoid vacuity and contributes to strut between interpterygoid and subtemporal vacuities (1); pterygoid markedly retracted so ectopterygoid makes a large contribution to strut between interpterygoid and subtemporal vacuities (2).

27. Ornament absent from ventral surface of the corpus of the parasphenoid and pterygoids (0); present in both parasphenoid and pterygoids, or at least in one of them (1).

28. Cultriform process of parasphenoid narrow and rounded (0); narrow and flat (1); broad and flat (2); broad, flat and expanded anteriorly between the vomers (3).

29. Vomerine depression or foramen just anterior to cultriform process of the parasphenoid, absent (0); present (1); present as a vacuity (2).

The presence of a vacuity in this position is scored for *Thabanchuia* as the region is not preserved in any specimen of *Tupilakosaurus*.

30. Corpus of the parasphenoid antero-posteriorly elongated (0); nearly as long as wide (1).

31. Median keel on cultriform process absent (0); median keel present throughout the length of the cultriform process (1); median keel developed on part of the cultriform process only (2).

32. Tooth row present on palatine and ectopterygoid (0); tooth row reduced (1); tooth row absent (2).

33. Ectopterygoid tusks absent (0); present (1).

34. Maximum width of interpterygoid vacuity pair less than 90% of their maximum length (0); width of pair greater than 90% of their length (1).

35. Subtemporal vacuity extends anteriorly less than half way up the interpterygoid vacuity or as far as the mid point of the vacuity (0); subtemporal vacuity extends anteriorly further than the mid point of the interpterygoid vacuity (1).

36. Occipital border of the quadrate ramus of the pterygoid sutures with quadrate (0); pterygoid does not suture with quadrate forming a lower palatoquadrate fissure (1).

37. Occipital portion of the ascending ramus of the pterygoid sutures with descending occipital flange of squamosal (0); reduced in height leaving an upper palatoquadrate fissure (1).

38. Exoccipital condyles elliptical, facing posteromedially (0); more rounded, facing posteriorly, held on short stalk (1).

39. Exoccipitals separated in the midline of the palate by the parasphenoid (0); exoccipitals contact or suture in the midline (1).

40. More than one distinct small foramen on lateral wall of exoccipital (0); an enlarged foramen on lateral wall of exoccipital (1).

41. Posttemporal fenestra markedly wider than deep (0); about as wide as deep or deeper than wide (1).

42. Paraquadrate foramen present on occipital portion of quadratojugal

(0); present on posteroventrolateral ornamented portion of quadratojugal (1); absent (2).

43. Occipital wall of squamosal and quadratojugal vertical or convex (0); vertically concave (squamosal-quadratojugal trough) (1).

44. Body of the pterygoid and quadrate ramus of the pterygoid curve smoothly onto occiput forming an oblique ridge (0); body of the pterygoid and quadrate ramus of the pterygoid form a sharp edge on occiput (1).

45. No substapedial ridge on posterodorsal surface of the pterygoid (0); substapedial ridge present (1).
This ridge is characteristic of chigutisaurids in which the area is preserved. It varies in shape in the different taxa.

46. Ascending ramus of the pterygoid forms a continuous curve with posterior edge of quadrate ramus (0); ascending ramus of the pterygoid arises from dorsal surface of the pterygoid as a shallow, curved lamina (1); ascending ramus of the pterygoid arises from dorsal surface of the pterygoid as a shallow, uncurved lamina (2); ascending ramus of the pterygoid arises from dorsal surface of the pterygoid as a gently concave lamina which is also recurved posteriorly in vertical section (3); ascending ramus of the pterygoid arises from dorsal surface of the pterygoid as a gently concave lamina (4).

47. Ascending ramus of the pterygoid thickened by an ascending column positioned towards its medial edge (0); column absent (1).

48. Exoccipital condyles not projected beyond the posterior margin of the skull table (0); exoccipital condyles projected well beyond the posterior margin of the skull table (1).

49. Vertical margin of the occipital portion of the squamosal, beside palatoquadrate fissure, smooth (0); flanged (1).
This flange is well developed in *Batrachosuchus browni* and a broken edge of the squamosal in the same position indicates that it was present in *B. watsoni.*

50. Chordatympanic foramen of the mandible present on prearticular-articular suture (0); chordatympanic foramen contained within prearticular (1); absent (2).

51. Mandibular sulcus of sensory canal absent from ornamented area of mandible (0); well-developed (1); slightly developed (2).

52. PGA (post glenoid area) of mandible undeveloped (0); PGA of mandible short (1); PGA of mandible slender, elongate (2); PGA of mandible slender, very elongate (3).

53. Articular forms lingual border of PGA (post glenoid area) of mandible (0); prearticular extends posteriorly on PGA of mandible so that the articular is exposed on the lingual wall posteriorly only (1); articular almost excluded from lingual wall by a posterior growth of the prearticular, thus restricted to a longitudinal tongue on the PGA (2); prearticular-surangular suture on the PGA so articular is completely excluded from the PGA (3).

54. Articular level with dentary tooth row (0); below level of dentary tooth row (1).

55. Posterior meckelian foramen bordered by the prearticular, postsplenial and angular (0); posterior meckelian foramen bordered by the prearticular and postsplenial alone (1); prearticular and angular alone (2).

56. Prearticular process (hamate process) in the mandible absent (0); slightly developed (1); well developed (2).

57. Teeth or denticles present on all coronoids (0); present on posterior and/or middle coronoids only (1); absent from all coronoids (2)

58. Transverse trough on the postglenoid area (PGA) just behind the glenoid area, present (0); absent (1).
The presence of a transverse trough is a synapomorphy of Dvinosauridae and Tupilakosauridae and absent from stereospondyls with an elongate PGA (Brachyopoidea).

59. Dorsal process of clavicle (prescapular process) short and with an anterior flange (0); without anterior flange and tall, with the tip of the process terminating above or just posterior to the posterior margin of the clavicular blade (1); without anterior flange and tall, with the tip of the process terminating well behind the posterior margin of the clavicular blade (2).
In brachyopoids the dorsal process of the clavicle arises from a narrow base at the postero-lateral point of the clavicular blade. In chigutisaurs it is initially perpendicular to the blade but may slope posteriorly toward the distal end. In brachyopids it slopes posteriorly from the base.

60. Ceratobranchials present in adult (0); lost in adult (1).

### APPENDIX 2

### Data Matrix of Brachyopoid Temnospondyls and Six Outgroups

The following taxa are presented in the matrix for information but not included in the analysis because of their fragmentary or immature status: *Platycepsion, Batrachosuchus concordi, Notobrachyops, Batrachosuchoides, Koolasuchus. Watsonisuchus* was scored from *W. (Parotosuchus) aliciae,* QMF14481 (Warren and Schroeder, 1995).

APPENDIX 3. Character-taxon matrix used in phylogenetic analysis.

| Taxon | Characters | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
| outgroup | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dvinosauridae | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | - | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | - | 0 | 3 | 1 | 0 |
| Tupilakosauridae | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 2 | 2 | - | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | ? | 0 | 1 | 0 | 3 | 2 | 0 |
| *Rhineceps* | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Watsonisuchus* | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| Rhytidosteidae | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 |
| *Brachyops* | 1 | 2 | 0 | ? | ? | ? | 1 | 1 | ? | ? | 2 | 2 | - | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | ? | 1 | 1 | 0 | 1 | 1 | 1 |
| *Bothriceps* | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | ? | ? | 1 | ? | ? | ? | ? | 1 | 0 | 0 | ? | 1 | 1 | 0 | ? | 1 | 1 | 1 | 0 | 0 | 1 |
| *Platycepsion* | 1 | 1 | 1 | 2 | ? | ? | 1 | ? | ? | 0 | 2 | 2 | - | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | ? | ? | ? | ? |
| *Batrachosuchus browni* | 1 | 2 | 0 | 2 | ? | ? | 1 | 1 | ? | ? | 2 | 2 | - | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | ? | 1 | ? | 1 | 2 | 1 | 1 |
| *Batrachosuchus watsoni* | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | ? | ? | 2 | 2 | - | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 2 | 1 | 1 |
| *Xenobrachyops* | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 2 | 2 | - | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 2 | 0 | 1 | 1 | 1 |
| *Batrachosuchus concordi* | 1 | 2 | 0 | 2 | 1 | 1 | 1 | ? | ? | ? | 2 | 2 | - | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 2 | ? | 1 |
| *Batrachosuchus henwoodi* | 1 | 2 | 1 | 2 | ? | ? | 1 | 1 | 0 | ? | 2 | 2 | - | ? | 0 | ? | 1 | 1 | 1 | 1 | 1 | 1 | ? | 2 | 1 | ? | 0 | 1 | ? | 1 |
| *Banksiops* | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 2 | - | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | ? | 1 | 2 | 1 | 1 |
| *Hadrokkosaurus* | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 2 | - | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | ? | 1 | 1 | 0 | 3 | 1 | 1 |
| *Notobrachyops* | 1 | - | 0 | 3 | 1 | 1 | 1 | ? | ? | ? | 2 | 2 | - | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Batrachosuchoides* | 1 | ? | - | 2 | 1 | 0 | 1 | 1 | 0 | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | 0 | ? | ? | ? | ? | ? | ? | ? | ? |
| *Sinobrachyops* | 1 | 2 | 0 | ? | 1 | ? | ? | 1 | ? | 1 | 2 | 2 | - | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Keratobrachyops australis* | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 |
| *Keratobrachyops* sp. | 1 | 2 | 0 | ? | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 |
| *Pelorocephalus* spp. | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Kuttycephalus* | 1 | 2 | 0 | 2 | 0 | ? | ? | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Compsocerops* | 1 | 2 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | ? | 1 |
| *Siderops* | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 |
| *Koolasuchus* | 1 | 2 | 0 | ? | ? | ? | 1 | ? | 0 | ? | 1 | 1 | 1 | 1 | ? | 0 | 1 | 1 | ? | ? | ? | 1 | 0 | 2 | ? | ? | ? | ? | ? | 1 |

APPENDIX 3. Continued.

| Taxon | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| outgroup | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Dvinosauridae | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | - | 0 | 0 | 0 | 1 | 1 | 0 | 1 | ? | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 |
| Tupilakosauridae | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | - | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | ? | 1 | 1 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 |
| *Rhineceps* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | ? | 1 |
| *Watsonisuchus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 |
| Rhytidosteidae | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| *Brachyops* | 2 | 1 | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | ? | ? | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 |
| *Bothriceps* | ? | ? | ? | 0 | 0 | 1 | 0 | 1 | 0 | ? | 1 | 2 | 1 | 1 | 0 | ? | ? | 0 | ? | 1 | 0 | 3 | 1 | 0 | ? | ? | ? | 1 | ? | 1 |
| *Platycepsion* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | ? |
| *Batrachosuchus browni* | 0 | 2 | 1 | 1 | 1 | 1 | ? | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | ? | ? | 1 | 1 | 2 | 0 | 3 | 2 | ? | ? | 1 | ? | 1 | 2 | 1 |
| *Batrachosuchus watsoni* | 0 | ? | ? | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 4 | 1 | 1 | 1 | 2 | 0 | 3 | 2 | ? | ? | 1 | ? | 1 | 2 | 1 |
| *Xenobrachyops* | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 4 | 1 | 0 | 0 | ? | 0 | 3 | 2 | 1 | ? | 0 | 1 | 1 | ? | 1 |
| *Batrachosuchus concordi* | 0 | ? | 1 | 1 | ? | 1 | 1 | 1 | 0 | 1 | 1 | ? | 1 | 1 | 0 | ? | ? | ? | ? | 2 | 0 | 3 | ? | 1 | ? | 0 | 2 | 1 | ? | ? |
| *Batrachosuchus henwoodi* | 0 | ? | 1 | 1 | 1 | 1 | 1 | ? | ? | ? | 1 | 2 | 1 | 1 | 0 | ? | ? | 1 | ? | 2 | 0 | 3 | 2 | 1 | 0 | ? | ? | 1 | ? | 1 |
| *Banksiops* | 0 | 2 | 1 | 1 | 1 | 1 | ? | 1 | 0 | ? | 0 | 2 | 1 | 1 | 0 | ? | ? | 1 | 0 | 2 | ? | 3 | 2 | 1 | 0 | 0 | ? | 1 | ? | 1 |
| *Hadrokkosaurus* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 4 | 1 | 1 | 0 | 2 | ? | 3 | 2 | 1 | 2 | 0 | 1 | 1 | 2 | 1 |
| *Notobrachyops* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 |
| *Batrachosuchoides* | ? | 1 | 1 | ? | ? | ? | ? | 0 | - | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 | 3 | ? | ? | ? | ? | ? | 1 | ? | 0 |
| *Sinobrachyops* | 0 | 0 | 1 | 1 | 1 | 1 | ? | 1 | 1 | ? | 1 | 0 | 1 | 1 | ? | ? | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 |
| *Keratobrachyops australis* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | ? | 1 |
| *Keratobrachyops* sp. | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | ? | ? | ? | 0 | 0 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 |
| *Pelorocephalus* spp. | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 0 | 2 | 3 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Kuttycephalus* | 0 | 1 | 1 | 0 | 0 | 0 | ? | 1 | ? | ? | 0 | 2 | 1 | 1 | ? | ? | ? | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 |
| *Compsocerops* | 0 | 0 | ? | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | ? | ? | ? | 1 | 0 | 1 | 0 | 3 | 2 | 0 | 1 | 1 | 2 | 1 | 1 | 1 |
| *Siderops* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | ? | ? | 3 | 0 | 1 | 1 | 1 | ? | 1 | 1 |
| *Koolasuchus* | ? | ? | ? | ? | 0 | 0 | 0 | 1 | ? | 1 | 0 | ? | ? | 1 | 1 | 3 | 0 | ? | ? | 1 | 0 | 2 | 3 | 0 | 1 | 1 | 2 | 1 | 1 | 1 |