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A BRACHYOPID TEMNOSPONDYL FROM THE LOWER *CYNOGNATHUS* ASSEMBLAGE ZONE IN THE NORTHERN KAROO BASIN, SOUTH AFRICA

by

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ABSTRACT

A new brachyopid temnospondyl is described from the Early to Middle Triassic *Cynognathus* Assemblage Zone of the upper Beaufort Group, Karoo Basin of South Africa. It is the fourth named brachyopid from the Karoo and the first from the northern part of the basin. Despite the incomplete nature of the holotype skull, the new brachyopid apparently shows closest affinities to *Batrachosuchus watsoni*. However, differences in the width of the sensory sulci, the absence of a transverse occipital sulcus, and the presence of a unique narial morphology, warrants separation at the species level. The holotype skull also provides insight into the morphology of the ventral surface of the skull roof and the configuration of the bones between the orbit and the nostril. A referred right mandibular ramus, the most complete yet recovered of a brachyopid, also shows several unique features. A reconsideration of the taxonomy of the brachyopid genus *Batrachosuchus* reveals that *Batrachosuchus watsoni* possesses several characters distinct from the type species, *Batrachosuchus browni*, and is thus transferred to a new genus. In addition, *'Batrachosuchus' henwoodi* and *Batrachosuchus concordi* probably do not pertain to the genus *Batrachosuchus*. Brachyopid diversity in the Karoo is exceeded only by the Mastodonsauridae and Rhinesuchidae, and they may eventually prove to be important aids in the biostratigraphy of the *Cynognathus* Assemblage Zone.

KEYWORDS: Brachyopidae, temnospondyl, *Cynognathus* Assemblage Zone, Triassic, Karoo

INTRODUCTION

Temnospondyls are remarkably well represented in the Mesozoic of South Africa, although the rocks of the Permo-Triassic Beaufort Group (Karoo Supergroup) of the Karoo Basin are renown primarily for their therapsid fauna. The overlying Triassic-Jurassic Stormberg Group is largely devoid of temnospondyls, although one higher-level taxon is present, the Chigutisauridae (Warren & Damiani 1999). The Permian record is considerably less diverse than the Triassic and represented by a single higher-level taxon, the Rhinesuchidae. Overall the South African Mesozoic temnospondyl record is amongst the most diverse in the world, with some 10 higher-level taxa present. These are the Amphibamidae, Brachyopidae, Chigutisauridae, Laidleriidae, Lydekkerinidae, Mastodonsauridae (the senior synonym of the 'Capitosauridae' (Damiani 2001a)), Rhinesuchidae, Rhytidosteidae, Trematosauridae and Tupilakosauridae. Two of these, the Amphibamidae and Tupilakosauridae, are representatives of the Palaeozoic lineages Dissorophoidea and Dvinosauria, respectively, the remaining higher-level taxa being members of the Stereospondyli.

Members of the higher-level taxon Brachyopidae are amongst the rarest of Mesozoic temnospondyls, with most occurring in the Early and Middle Triassic of Gondwana (Warren & Marsicano 2000), although a possible Late Triassic brachyopid has been identified from Argentina (Marsicano *et al.* 2000). Slightly younger brachyopids are known from Asia and Eastern Europe where they are known to have survived into the Jurassic (Warren *et al.* 1997). The range of sizes in skull length vary between just over 2 cm in the juvenile *Platycepsion wilkinsoni* (Warren & Marsicano 1998) to 30 cm in *Vigilius wellesi* (Welles & Estes 1969), although fragmentary remains indicative of much larger individuals are known. Brachyopids are characterised by short, broad parabolic skulls, anteriorly placed orbits, well-defined sensory canals on the skull roof (indicating a primarily aquatic habitat), posteriorly projecting occipital condyles, an elongate post-glenoid area of the mandible, and down-turned quadrate rami of the pterygoids resulting in unusually deep cheeks. These characters imply that brachyopids were active hunters that had especially strong jaw muscles and a powerful bite (Warren 2000).

The phylogenetic position of the Brachyopidae within the Temnospondyli remains contentious. The Brachyopidae has been considered a derived member of the monophyletic Stereospondyli by some authors (Yates & Warren 2000; Warren & Marsicano 2000), while others ally the brachyopids with various Palaeozoic taxa which fall outside of the Stereospondyli, including the Tupilakosauridae, Dvinosauridae, and 'Saurerpetontidae' (Watson 1956; Coldiron 1978; Foreman 1990; Milner 1990; Shishkin 1991; Damiani & Warren 1996; Schoch & Milner 2000). This issue will not be discussed further as it is beyond the scope of this paper.

In South Africa the Brachyopidae is represented by three nominal taxa from the Early to Middle Triassic *Cynognathus* Assemblage Zone of the Beaufort Group, *Batrachosuchus browni* (Broom 1903), *B. watsoni*

(Watson 1919; Haughton 1925), and an as yet unpublished new taxon (Damiani & Kitching in press). *Batrachosuchus browni* is known from a near-complete skull which was recovered from an unknown locality in the Aliwal North District, Eastern Cape Province; *B. watsoni*, which is also known from a near-complete skull, is presumed to have been recovered from a locality in the nearby Burgersdorp District, Eastern Cape Province. Given the uncertain locality data, and as both the lower (Subzone A) and middle (Subzone B) parts of the *Cynognathus* biozone are exposed in these districts (Hancox 2000), both taxa could pertain to either horizon within the *Cynognathus* biozone. The third taxon (Damiani & Kitching in press) is represented by a partial skull and two left mandibular rami that were recovered from a locality in the Burgersdorp District which pertains to the middle part of the *Cynognathus* biozone. These localities all occur in 'classic' (i.e. probably Subzone B) exposures of the *Cynognathus* Assemblage Zone in the south of the Karoo Basin. Additional fragmentary brachyopid cranial and postcranial material has been recovered from several localities in the *Cynognathus* biozone in the south of the basin and assigned to *Batrachosuchus* (Watson 1956; Welles & Estes 1969; Colbert & Cosgriff 1974; Warren & Marsicano 2000). No brachyopid material is as yet known from the underlying Early Triassic *Lystrosaurus* Assemblage Zone.

This paper describes a new species of brachyopid from the lower part of the *Cynognathus* Assemblage Zone in the northeastern Free State. It represents the fourth brachyopid species to be named from the Karoo and the first from the northern part of the Karoo Basin. The new brachyopid is represented by a partial skull roof and a complete right mandibular ramus and is compared especially to the other three named brachyopids from the Karoo. In addition, the taxonomy of the genus *Batrachosuchus* is re-evaluated in light of the discovery of the new brachyopid.

THE GENUS *BATRACHOSUCHUS*

The relationship of the two South African *Batrachosuchus* species has been an issue of some contention. Earlier workers (Watson 1956; Welles & Estes 1969) retained them as separate species largely on the basis of skull proportions, but in Warren and Marsicano's (2000) phylogenetic analysis of brachyopoids they grouped as sister-species, prompting Warren & Marsicano to suggest that *Batrachosuchus watsoni* may be a junior synonym of *B. browni*. The same sister-species relationship between *B. watsoni* and *B. browni* was found by Damiani & Kitching (in press), who used a data matrix modified from Warren & Marsicano (2000). In the course of attempting to determine the affinities of the new brachyopid (BP/1/5790), it was found necessary to critically re-examine the characters separating *Batrachosuchus browni* (Broom 1903) from *B. watsoni* (Haughton 1925). This was based on an examination of the holotype of *Batrachosuchus browni* (SAM-PK-5868) and photographs and specimen notes of the holotype of *B. watsoni* (BMNH R3589).

The skull of *Batrachosuchus browni* (Broom 1903; Watson 1956; Welles & Estes 1969; Chernin 1977) can be diagnosed by the presence of radiating, ridge-groove type dermal sculpturing, frontals which terminate level with the posterior margin of the orbits, an interfrontal, and a distinctive sensory sulci morphology as follows. The sensory sulci are relatively narrow throughout, the supraorbital sulcus has a broad outward curve between the orbits and the nostrils and a distinct medial curve towards the midline on the frontals prior to termination, and a shorter, accessory temporal sulcus which terminates on the anterior-most part of the supratemporal is present. The palate is characterised by a distinct vomerine foramen anterior to the cultriform process of the parasphenoid, ornament on the corpus of the parasphenoid, the lack of separation by the parasphenoid of the exoccipitals posteriorly, and the palatines forming most of the posterior margin of the choanae. The occiput is characterised by an extreme posterior projection of the occipital condyles behind the posterior margin of the skull roof.

In contrast, *Batrachosuchus watsoni* (Watson 1919, 1956; Haughton 1925; Welles & Estes 1969) differs markedly from *B. browni* in possessing uniform, pitted dermal sculpturing, frontals that terminate far behind the posterior margin of the orbits, and in lacking an interfrontal. Also, the sensory sulci are relatively wide, the supraorbital sulcus forms a sharper angle between the orbits and the nostrils and follows a straighter path on the frontals, there is no accessory temporal sulcus, and a discontinuous occipital sulcus is present on the tabulars and postparietals. The palate of *Batrachosuchus watsoni* lacks a vomerine foramen, the exoccipitals are separated by the parasphenoids posteriorly, the posterior margin of the choanae are formed almost entirely by the vomers, and the corpus of the parasphenoid appears to lack ornament. The occiput of *Batrachosuchus watsoni* is characterised by a markedly shorter posterior projection of the occipital condyles behind the posterior margin of the skull roof.

In considering the purported differences between *Batrachosuchus browni* and *B. watsoni*, Warren & Marsicano (2000) criticised earlier workers (Watson 1956; Welles & Estes 1969) who separated the species largely on skull proportions. This criticism is justifiable because skull size and shape can alter dramatically with ontogeny in temnospondyls (Boy & Sues 2000) and slight differences in proportions may be expected amongst adults of the same species. Chernin (1977) cited the presence of an interfrontal, a vomerine foramen, and narrower sensory canals in *B. browni* as important characters separating it from *B. watsoni*. However, Warren & Marsicano (2000) noted that an interfrontal is present in some clearly unrelated temnospondyl taxa, considered the width of the sensory canals to be somewhat subjective, and suggested that the vomerine foramen may be a depression filled with

matrix. The first two of these criticisms may be justifiable but the vomerine foramen in *Batrachosuchus browni* is undoubtedly a foramen and clearly different to the depression in *B. watsoni*. These criticisms notwithstanding, the sum of characters listed above appears to be of more than specific significance and warrant generic separation of *Batrachosuchus watsoni* from *B. browni*, as alluded to by Welles & Estes (1969) and Chernin (1977). Accordingly, *Batrachosuchus watsoni* is below placed in a new genus.

Two other brachyopid species previously assigned to the genus *Batrachosuchus* have also been reassessed during the course of this study. The first, *Batrachosuchus concordi* (Chernin 1977), is based on a small skull with associated lower jaws and postcranial material from the Upper Horizon of the N'tawere Formation at 'locality 15' near Sitwe in the Upper Luangwa Valley, Zambia (Drysdall & Kitching 1963), which is of Anisian age (Hancox 2000). Although poorly preserved, the skull of *B. concordi* appears to share with *Batrachosuchus browni* the presence of ridge-groove type dermal ornament, narrow sensory sulci, and frontals which probably terminate level with the posterior edge of the orbits. It shares with *'B'. watsoni* the possible presence of an occipital sulcus and separation of the exoccipitals by the parasphenoid. The presence or absence of an interfrontal, vomerine foramen, and ornament on the corpus of the parasphenoid is indeterminate because of poor preservation. However, contrary to Chernin (1977) and Warren & Marsicano (2000), the exoccipital condyles probably projected well beyond the posterior skull margin in the usual brachyopid fashion, this area having been affected by compaction. *Batrachosuchus concordi* appears to differ from both *B. browni* and *'B'. watsoni* in that the pineal is situated closer to the posterior margin of the orbits than to the posterior margin of the skull, and the sensory sulci are not well impressed and defined by a series of shallow pits. In addition, the supraorbital sulcus is continuous around the orbit posteriorly. According to Warren & Marsicano (2000), the small skull size, extremely large orbits, and lack of interlocking sutures indicate its probable juvenile nature. However, the orbits do not appear particularly large relative to the size of the skull and the lack of interlocking sutures may be an artifact of the extremely poor preservation of the skull. *Batrachosuchus concordi* probably does not pertain to the genus *Batrachosuchus* and will be the subject of a forthcoming redescription by the authors.

'Blinasaurus' henwoodi, the most recent species to be assigned to *Batrachosuchus*, was originally described by Cosgriff (1969) and is based on a poorly preserved skull and lower jaw material from the Early Triassic Blina Shale of Western Australia. Cosgriff (1969) reconstructed the skull as having a lacrimal, frontals entering the orbital margins, and extremely large orbits. Warren & Marsicano (1998) redescribed the holotype skull of *'B'. henwoodi* and amended Cosgriff's reconstruction by showing that a lacrimal was probably absent, the frontals were excluded from the orbital margins by a prefrontal-postfrontal contact, and the orbits were somewhat smaller than previously indicated although still large relative to the size of the skull. The resulting reconstruction showed a 'typical' brachyopid which Warren & Marsicano (1998) considered to be most closely related to the genus *Batrachosuchus*. Thus Warren & Marsicano transferred *'B'. henwoodi* to *Batrachosuchus* as they could find no autapomorphies to justify a new genus, but used the larger orbits of *'B'. henwoodi* to separate it at the species level. The holotype skull of *'B'. henwoodi* remains too poorly preserved for a definitive diagnosis although the nature of the supraorbital sulcus which is continuous with the infraorbital sulcus behind the orbits, and, in particular, the very large orbits, renders its referal to *Batrachosuchus* unlikely. However, *'Batrachosuchus' henwoodi* cannot be returned to *'Blinasaurus'* as the latter name remains a junior synonym of the name *Platycepsion* (Kuhn 1961; Warren & Marsicano 1998). For the moment, therefore, *'Batrachosuchus' henwoodi* should be regarded as *incertae sedis* within the Brachyopidae.

Finally, the brachyopid described in this paper has proved difficult to place taxonomically because it is represented by only a partial skull roof (BP/1/5790) and a mandible (BP/1/5883), rendering comparisons with the more complete brachyopids from the Karoo difficult. In addition, the skull roof is typically the most conservative aspect of the brachyopid skull. The skull roof shares apomorphic characters with both *Batrachosuchus browni* and *'Batrachosuchus' watsoni*, but is phenetically most similar to the latter, while the mandible possesses a number of characters not known in any other brachyopid mandible. The new brachyopid is considered to be congeneric with *'B'. watsoni* for reasons outlined below; however, it appears to possess a number of autapomorphies of the skull roof and mandible which warrants its description as a new species.

MATERIALS AND METHODS

BP/1/5790 consists of most of the skull roof and a small portion of the occiput of an adult brachyopid, and was found by J. Neveling on the farm Driefontein in the Paul Roux District, Free State Province, in February of 2000. Additional fragments of the skull were collected by the authors during a subsequent trip to the locality in April 2001. BP/1/5883, a complete right mandibular ramus, was found by the senior author during this subsequent trip. The strata at this locality belong to the lower part (Subzone A, upper Olenekian) of the *Cynognathus* Assemblage Zone (Upper Beaufort Group).

Both specimens were found imbedded at the base of an approximately 30 cm thick, bluish-grey, fine-grained sandstone layer, immediately above typical red-green mudstone of the *Cynognathus* Assemblage Zone. In the field these were consolidated with a dilute Glyptal

solution before being either directly removed in sections (skull) or plastered (mandible). In the laboratory the bulk of the matrix was removed mechanically using an airscribe, with subsequent finer preparation achieved using a hand-held pin-vice. The prepared surfaces were cleaned using a paint-brush and water, and cyanoacrylate glue used to join broken bone.

Comparative material examined in this study includes the type specimens of *Batrachosuchus browni* (SAM-PK-5868), *Batrachosuchus concordi* (BP/1/3728), and the new brachyopid of Damiani & Kitching (in press), henceforth referred to by its holotype number, BP/1/4004.

GEOLOGICAL SETTING

The Beaufort Group of the Karoo Basin preserves a complete Late Permian to early Middle Triassic sedimentary seqeunce and associated vertebrate fauna (Rubidge 1995; Hancox & Rubidge 1997), and has long been recognised as the global standard for the non-marine Permo-Triassic (Romer 1975; Cosgriff 1984; Lucas 1998). The Beaufort Group strata are fluvially derived and typically consist of alternating mudstone and sandstone units with characteristic upward-fining textures, red and purple colours, abundant vertebrate fossils, dessication cracks and palaeosol horizons, suggesting sediment accumulation on vast, semi-arid alluvial plains by floodplain aggradation (Smith 1990).The abundant and diverse vertebrate fauna is dominated by therapsids (Kitching 1977) which, combined with the paucity of basin-wide lithostratigraphic markers, have been used for the biostratigraphic subdivision of the group and stratigraphic correlation with faunas elsewhere (Kitching 1977; Keyser and Smith 1979; Rubidge 1995).

The *Cynognathus* Assemblage Zone, the uppermost biozone of the Beaufort Group, occupies the upper two-thirds of the Burgersdorp Formation in the south of the basin, and is widely exposed in the Queenstown, Burgersdorp, Aliwal North and Rouxville districts, reaching a maximum thickness of 600 m (Kitching 1995). A fauna assignable to the *Cynognathus* biozone has also recently been found in the north of the basin, in strata of the Driekoppen Formation, the northern equivalent of the Burgersdorp Formation (Welman *et al.* 1991). However, the biozone reaches a maximum thickness of only 60 m in this area (Hancox 2000). The Burgersdorp Formation is a predominantly argillaceous sequence and consists of thick, upward-fining units of laterally inextensive, olive-grey, fine- to medium-grained sandstones overlain by red-maroon coloured siltstones and mudstones and are thought to represent mixed-load meandering river and floodplain deposits (Kitching 1995; Hancox 1998, 2000). In contrast, the Driekoppen Formation has been interpreted as representing more widespread lacustrine or palustrine condition based on the lack of well-defined channel sandstones and limited occurrence of pedogenic calcareous concretions (Welman *et al.* 1991; Groenewald *et al.* 2001). Overall the rocks of the *Cynognathus* Assemblage Zone were deposited by anastomosed or frequently avulsing north-westerly to northerly flowing meandering streams with sandy channels and abundant crevasse splays onto thick subaerially exposed floodplain deposits under a semi-arid climate (Kitching 1995; Hancox 1998, 2000). Bone fragments in the *Cynognathus* Assemblage Zone are frequently found as dispersed and isolated specimens in mudrock units but may also occur in abundance in localised bonebeds, while more complete specimens occasionally occur in fine to medium-grained sandstone lenses (Kitching 1995).

Based largely on the spatial and temporal distribution of mastodonsaurid temnospondyls, the *Cynognathus* Assemblage Zone has been subdivided into three subzones whose ages have been determined mainly by correlation with more reliably dated faunas elsewhere (Hancox *et al.* 1995; Shishkin *et al.* 1995; Hancox 2000). The lowermost zone (subzone A, upper Olenekian) is predominantly exposed in the north of the basin and is defined by the first appearance datum of *'Kestrosaurus'*, which occurs in association with the temnospondyls *Parotosuchus*, *Trematosuchus*, and the new brachyopid described in this paper, and an as yet undescribed erythrosuchid archosauriform (Shishkin & Welman 1994; Hancox *et al.* 1995; Damiani 1999; Hancox 2000). The middle zone (subzone B, early Anisian) occurs within classic *Cynognathus* Assemblage Zone exposures in the south of the basin. *'Parotosuchus' africanus* is the amphibian index taxon and occurs in association with the dicynodont *Kannemeyeria* and the archosauriform *Erythrosuchus* (Hancox *et al.* 1995; Hancox 2000). Lastly, a very reduced upper zone (subzone C, late Anisian), restricted to the southern-most reaches of the basin, is characterised by the presence of the derived mastodonsaurid *Paracyclotosaurus*, which occurs in association with the dicynodonts *Angonisaurus* and *Shansiodon* (Hancox & Rubidge 1996; Hancox 2000; Hancox *et al.* 2000). Thus contrary to previous opinion which held that the *Cynognathus* biozone was either of Early (e.g. Anderson & Cruickshank 1978; Cosgriff 1984) or Middle Triassic (e.g. Ochev and Shishkin 1989) age, it is now considered to straddle the Early-Middle Triassic boundary.

SYSTEMATIC PALAEONTOLOGY

TEMNOSPONDYLI Zittel 1887-1890 *sensu* Laurin 1998

BRACHYOPOIDEA Lydekker 1885

BRACHYOPIDAE Lydekker 1885

BATHIGNATHUS gen. nov.

Batrachosuchus Haughton 1925, in part

Type Species. Bathignathus watsoni (Haughton) *gen. nov.*

Type Locality and Horizon. Bathignathus watsoni was recovered from an unknown locality, but Watson (1956) stated that this was most likely to have been the

Burgersdorp District (Eastern Cape Province) of the Karoo, and thus from the *Cynognathus* Assemblage Zone (Early-Middle Triassic) which is widely exposed in this area.

Etymology. From the Greek *bathys*, meaning 'deep', and *gnathos*, meaning 'jaw', in reference to the exceptionally deep jaw of brachyopids which results from the downturned quadrate rami of the pterygoids.

Referred Species. Bathignathus poikilops sp. nov.

Diagnosis. Distinguished from *Batrachosuchus* and all other brachyopids by the following combination of characters: dermal sculpturing consisting exclusively of uniform, rounded pitting; frontals terminate far behind the posterior margin of the orbits; interfrontal absent; sensory sulci relatively wide; supraorbital sulcus forms a sharp angle between the orbits and the nostrils and follows a relatively straight path on the frontals; accessory temporal sulcus absent; discontinuous transverse occipital sulcus present on the tabulars and postparietals; vomerine foramen absent; exoccipitals separated by the parasphenoid posteriorly; posterior margin of the choanae formed almost entirely by the vomers; corpus of the parasphenoid lacks ornament; short posterior projection of the occipital condyles behind the posterior margin of the skull roof.

BATHIGNATHUS POIKILOPS sp.nov.

Holotype. BP/1/5790, a partial skull roof and part of the occiput.

Locality and Horizon. Farm Driefontein, Paul Roux District, north-eastern Free State Province, South Africa; lower *Cynognathus* Assemblage Zone (subzone A, upper Olenekian), Upper Beaufort Group, northern Karoo Basin. This locality has yielded a diverse vertebrate fauna that includes the temnospondyls *'Kestrosaurus'* and *Parotosuchus* (Damiani 1999, 2001b), the enigmatic ?diapsid *Palacrodon* (Gow 1999), and undescribed procolophonid, archosauriform, cynodont and fish material.

Etymology. From the Greek *poikilos*, meaning 'mottled', and *opsis*, meaning 'face', in reference to the mottled colour preservation of the bone of the skull roof.

Referred material. BP/1/5883, a complete right brachyopid mandibular ramus. This specimen was recovered some 20 m away from the holotype skull and was also imbedded at the base of a narrow, fine-grained sandstone layer immediately above the typical red-green mudrock at Driefontein. BP/1/5883 is referred to *Bathignathus poikilops* because it was recovered in close proximity, is of a comparable size to the holotype skull (BP/1/5790), and there are no indications that more than one brachyopid species is present at Driefontein.

Diagnosis. Of the characters diagnosing the genus *Bathignathus*, *B. poikilops* departs from it only in having narrower sensory canals and in lacking a transverse occipital sulcus, but is identical in all other observable characters. Thus *B. poikilops* is provisionally referred to *Bathignathus* because of its phenetic similarity to *Bathignathus watsoni* and because it seems less prudent to establish a new genus based solely on a partial skull roof. However, the skull of *B. poikilops* can be distinguished from *B. watsoni* and all other brachyopids in the possession of at least one autapomorphy, namely the morphology of the nostrils which consists of an exceptionally large, outer *naris externa* and a smaller, inner *naris proprieta*. The mandible of *B. poikilops* can be distinguished from those of all other brachyopids by the following combination of characters: labial wall of adductor fossa massive; postsymphyseal foramen massive; ridge present on posterior coronoid; coronoid teeth absent; posterior meckelian foramen bordered by postsplenial and prearticular only. The latter two characters appear to represent autapomorphies of *B. poikilops*.

DESCRIPTION

Skull roof – dorsal surface

(Figures 1A, 2A, 3)

The skull roof is well preserved and includes a portion of the left skull margin between the nostril and orbit, the complete left orbit and the medial margin of the right orbit, the postero-lateral edge of the left nostril, and a small section of the posterior skull margin and occiput. The overall shape of the skull of *Bathignathus poikilops* is typically brachyopid in being short, broad and parabolic in outline. The postero-lateral margins of the skull roof appear to have sloped slightly anteriorly, as in *Bathignathus watsoni* (Watson 1956), *Batrachosuchus browni* (Chernin 1977), and BP/1/4004 (Damiani & Kitching in press). This condition differs from that in basal brachyopids such as *Brachyops laticeps* (Warren & Marsicano 2000) and *Xenobrachyops allos* (Damiani & Warren 1996) in which this margin is straight.

Dermal bone of the skull roof is generally 5 mm in thickness throughout except posteriorly where it doubles in thickness to around 10 mm near the rear skull margin. The surface of the bone bears the usual temnospondyl dermal sculpturing which consists almost exclusively of well-defined, sub-circular to circular pits, with minimal ridge-groove development. The sensory sulci are well defined on all areas of the skull roof and have an average width of around 5 mm and an average depth of around 2 mm, with a U-shaped cross-section. The morphology of the sensory sulci in *Bathignathus poikilops* is similar to that of *Batrachosuchus browni* except that *B. poikilops* lacks an accessory temporal sulcus and the supraorbital sulcus lacks the distinct medial curve toward the midline on the frontals as seen in *B. browni* (Chernin 1977). In contrast, the course of the sensory sulci of

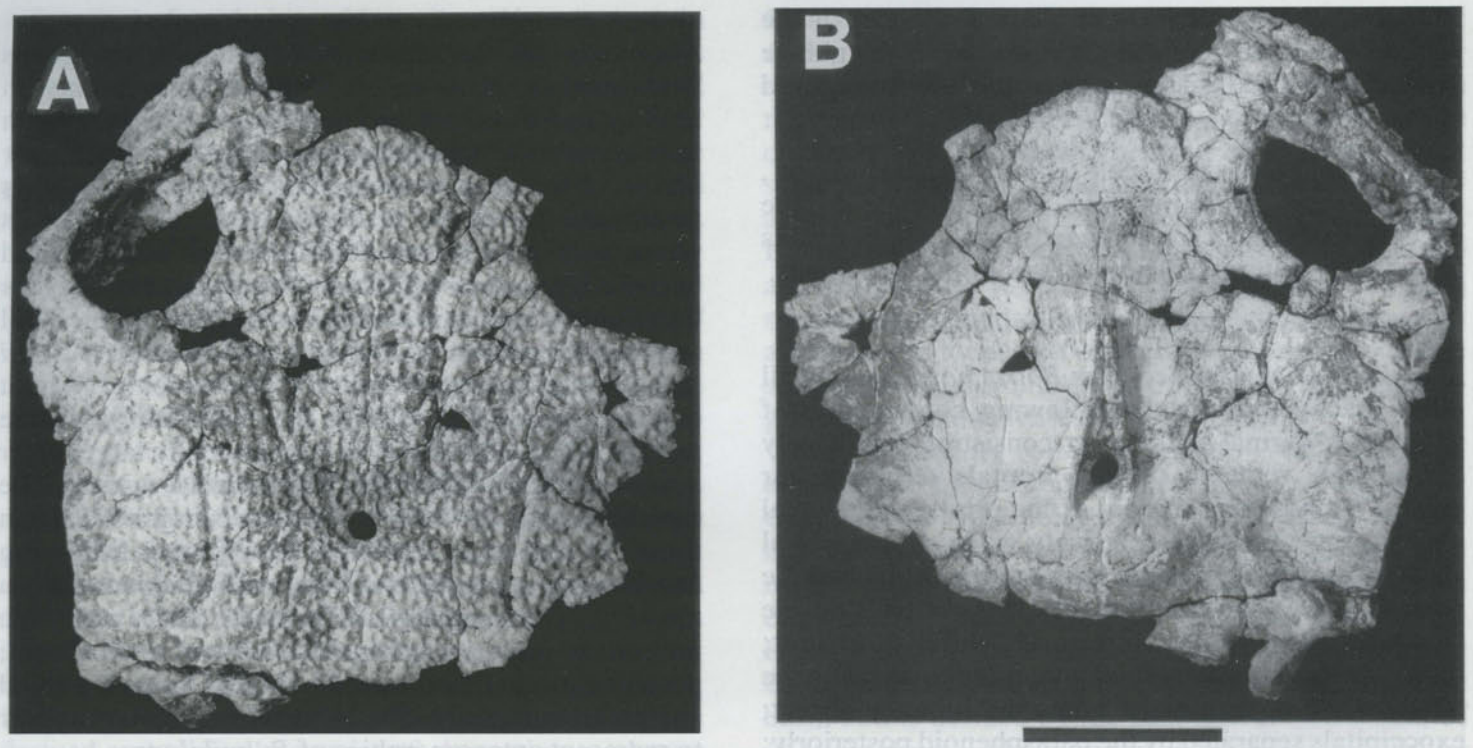

Figure 1. *Bathignathus poikilops sp. nov.* (BP/1/5790), photographs of the skull roof in A, dorsal and B, ventral views. Scale bar equals 50 mm.

B. poikilops is identical to that of *Bathignathus watsoni* except that in the latter the sensory sulci are wider, V-shaped in cross-section, and a transverse occipital sulcus is present (Watson 1956).

Only a small portion of the left nostril is preserved, but is distinctive in having a very large outer margin confluent with the surface of the skull roof (here termed the *naris externa*), and an inner, countersunk surface with a smaller curved margin that presumably represents the edge of the true nostril (here termed the *naris proprieta*). The bone forming this inner surface cannot be determined but it does not appear to form part of the septomaxilla, which forms a separate element of the skull roof (see below). The margin of the *naris externa* is formed postero-medially by the nasal, postero-laterally by the septomaxilla, laterally by the maxilla, and anteriorly presumably by the premaxilla. By extrapolation from the preserved narial margins the nostrils were undoubtedly very large and located close to the skull midline and presumably also to the anterior skull margin. The overall morphology of the nostril in *Bathignathus poikilops* with the distinctive 'double' margin appears to be unique within the Brachyopidae. In most brachyopids in which the area is well preserved the nostril is small and rounded and corresponds to the *naris proprieta* of *B. poikilops*.

Sutures on the skull roof are clear and well defined, allowing for easy identification of the skull bones which show an arrangement that is generally similar to that of other brachyopids. As this arrangement is clearly shown in the diagrams, only a few notable features will be described. As with virtually all other brachyopids in which the area is well preserved a septomaxilla is present; it forms a discrete element of the skull roof bordering the *naris externa*. In *Bathignathus poikilops* the septomaxilla is wedge-shaped, ornamented, and is crossed by the infraorbital sulcus. In contrast, the septomaxilla of most other brachyopids, where present, usually occupies part of the posterior wall of the nostril with perhaps a small contribution to the skull roof (Damiani & Warren 1996; Warren & Marsicano 1998, 2000), but is never crossed by the infraorbital sulcus.

Despite the presence of a septomaxilla, the maxilla of *Bathignathus poikilops* makes a large contribution to the margin of the *naris externa*, perhaps due, in part, to the large size of the latter. This contrasts with the condition in most other brachyopids in which a septomaxilla is present, including *Bathignathus watsoni*, where the maxilla is excluded from or makes only point contact with the narial margin anterior to the septomaxilla (Damiani & Warren 1996; Warren & Marsicano 1998, 2000). However, in those brachyopids in which a septomaxilla appears to be absent the maxilla broadly enters the narial margin (Warren & Marsicano 2000). The condition in *Batrachosuchus browni* cannot be determined because of lack of preservation, contrary to Chernin (1977).

The area lateral to the orbits and between the orbits and the nostrils is rarely well preserved in brachyopids, so that the arrangement of bones in this area, including the presence or absence of a lacrimal, is seldom certain (Damiani & Warren 1996). Fortunately this area is well preserved in *Bathignathus poikilops*, and a lacrimal is clearly absent. The jugal extends anteriorly to suture with the prefrontal on the anterior margin of the orbit, thereby excluding the maxilla from entering the orbital margin. This condition appears to be the case in most brachyopids in which sutures in this area are shown (Warren & Marsicano 2000). The condition is indeterminate in *Bathignathus watsoni* (Watson 1956) and *Batrachosuchus browni* (contra Chernin 1977) because of lack of preservation. There is no trace of a

lateral exposure of the palatine (LEP) on the orbital margin as has been reported in *Xenobrachyops allos* and *Sinobrachyops placenticephalus* (Damiani & Warren 1996).

Finally, examination of the frontal bones in members of the Brachyopidae from the Karoo reveals that in *Bathignathus poikilops* and *B. watsoni* (Watson 1956) the frontal bones terminate well behind the posterior margin of the orbits. In contrast, in *Batrachosuchus browni* (Chernin 1977) the frontal bones terminate at approximately the same level as the orbits. The latter condition also occurs in '*Batrachosuchus*' *henwoodi* (Warren & Marsicano 1998). However, this character may be dependant on the size of the animal and thus be related to ontogeny.

Skull roof – ventral surface

(Figures 1B, 2B)

The ventral surface of the skull roof of *Bathignathus poikilops* is well preserved, allowing its description for the first time in a brachyopid. Sutures on this surface are generally clearly visible although they do not always correspond directly with the sutures on the dorsal surface, as there may be considerable overlapping of

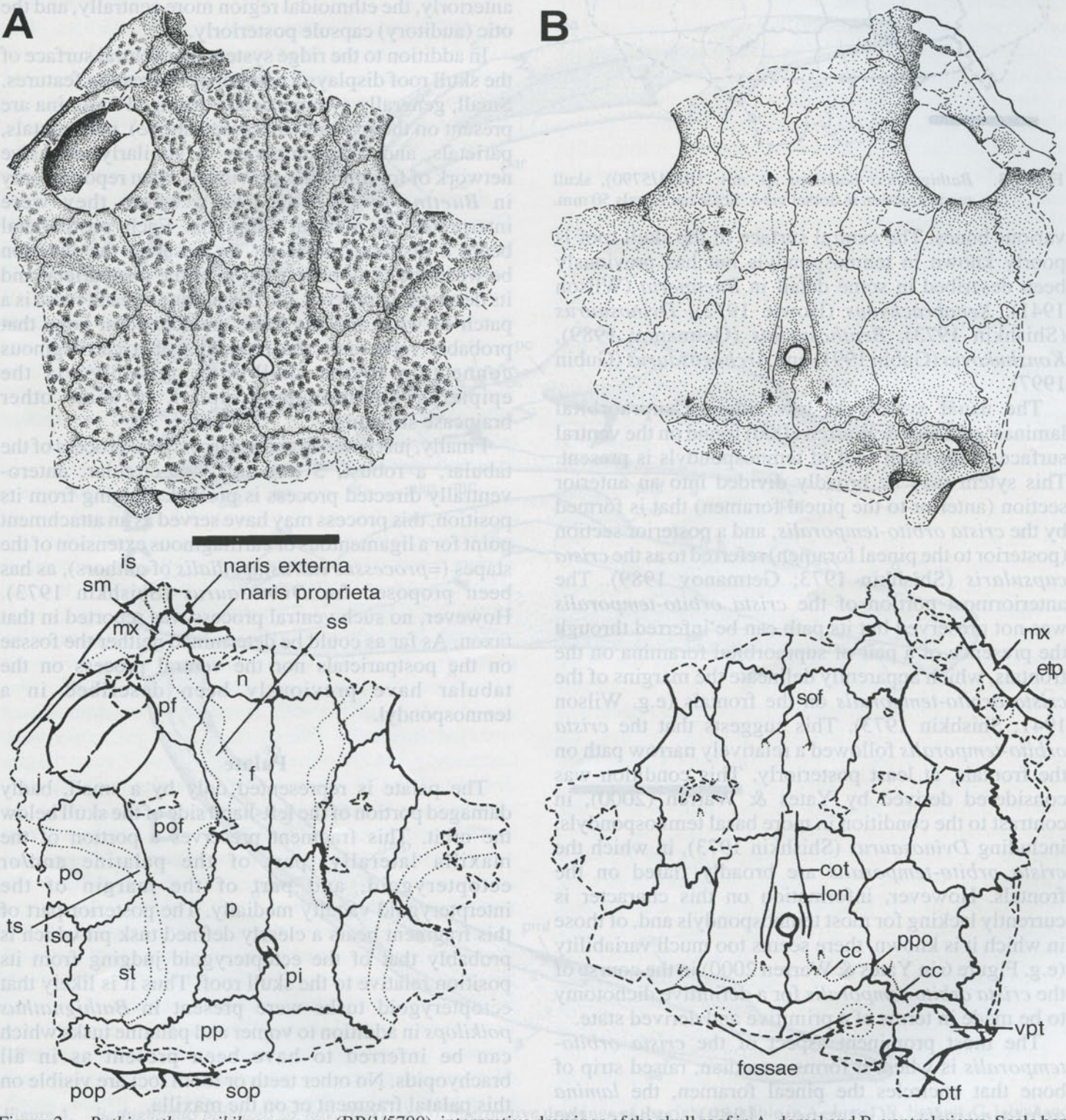

Figure 2. *Bathignathus poikilops sp. nov.* (BP/1/5790), interpretive drawings of the skull roof in A, dorsal and B, ventral views. Scale bar equals 50 mm.

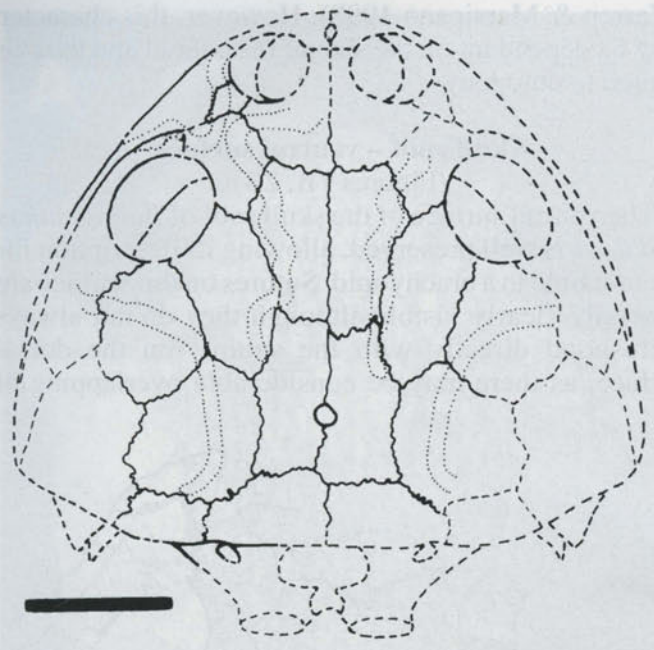

Figure 3. *Bathignathus poikilops sp. nov.* (BP/1/5790), skull reconstruction in dorsal view. Scale bar equals 50 mm.

various bones. The ventral surface of the skull roof is poorly known in temnospondyls but has previously been described in some detail in *Buettneria* (Wilson 1941), *Xenobrachyops* (Howie 1972), *Dvinosaurus* (Shishkin 1973), *Benthosuchus* (Getmanov 1989), *Konzhukovia* (Gubin 1991) and *Archegosaurus* (Gubin 1997).

The usual system of low ridges ('supraorbital laminae' of Yates & Warren 2000) found on the ventral surface of the skull roof of temnospondyls is present. This sytem may be broadly divided into an anterior section (anterior to the pineal foramen) that is formed by the *crista orbito-temporalis*, and a posterior section (posterior to the pineal foramen) referred to as the *crista capsularis* (Shishkin 1973; Getmanov 1989). The anteriormost portion of the *crista orbito-temporalis* was not preserved but its path can be inferred through the presence of a pair of supraorbital foramina on the frontals, which apparently delineate the margins of the *crista orbito-temporalis* on the frontals (e.g. Wilson 1941; Shishkin 1973). This suggests that the *crista orbito-temporalis* followed a relatively narrow path on the frontals, at least posteriorly. This condition was considered derived by Yates & Warren (2000), in contrast to the condition in more basal temnospondyls, including *Dvinosaurus* (Shishkin 1973), in which the *crista orbito-temporalis* are broadly flared on the frontals. However, information on this character is currently lacking for most temnospondyls and, of those in which it is known, there seems too much variability (e.g. Figure 6 in Yates & Warren 2000) in the course of the *crista orbito-temporalis* for a definitive dichotomy to be made in terms of a primitive and derived state.

The most prominent aspect of the *crista orbito-temporalis* is where it forms a median, raised strip of bone that encircles the pineal foramen, the *lamina orbito-nasalis* (Getmanov 1989), where the sphenethmoid cartilage attached to the skull roof (Shishkin 1973). The posteriormost portion of this lamina is slightly asymmetrical around the pineal foramen in that the cristae do not terminate at the same transverse level. Posterior to the *lamina orbito-nasalis* the ridges diminish in height and follow a transverse sigmoidal path across the parietal and supratemporal bones before terminating near the supratemporal-tabular suture; this system is referred to as the *crista capsularis* (Shishkin 1973). The entire ridge system of *crista orbito-temporalis* anteriorly and centrally and *crista capsularis* posteriorly delimited the soft cartilage of the neurocranium (e.g. Wilson 1941; Shishkin 1973), which comprised the olfactory (nasal) capsule anteriorly, the ethmoidal region more centrally, and the otic (auditory) capsule posteriorly.

In addition to the ridge system, the ventral surface of the skull roof displays a number of interesting features. Small, generally symmetrically arranged foramina are present on the frontals (discussed above), postfrontals, parietals, and supratemporals. A similarly extensive network of foramina has previously been reported only in *Buettneria* (Wilson 1941), where they were interpreted as nutrient foramina. Each postparietal bears a distinct, round pit or fossa on the junction between the skull table portion of the postparietal and its descending process. On the surface of each fossa is a patch of what appears to be endochondral bone that probably represents the remnants of a cartilaginous connection to the skull roof, possibly via the epipterygoid, the supraoccipital, or some other braincase structure.

Finally, just anterior to the paroccipital process of the tabular, a robust, 5 mm tall, sub-circular, antero-ventrally directed process is present. Judging from its position, this process may have served as an attachment point for a ligamentous or cartilaginous extension of the stapes (=*processus extrastapedialis* of authors), as has been proposed for *Dvinosaurus* (Shishkin 1973). However, no such ventral process was reported in that taxon. As far as could be determined neither the fossae on the postparietals nor the ventral process on the tabular have previously been described in a temnospondyl.

Palate

The palate is represented only by a small, badly damaged portion of the left-hand side of the skull below the orbit. This fragment preserves a portion of the maxilla laterally, part of the palatine and/or ectopterygoid, and part of the margin of the interpterygoid vacuity medially. The posterior part of this fragment bears a clearly defined tusk pit which is probably that of the ectopterygoid judging from its position relative to the skull roof. Thus it is likely that ectopterygoid tusks were present in *Bathignathus poikilops* in addition to vomer and palatine tusks which can be inferred to have been present as in all brachyopids. No other teeth or tooth loci are visible on this palatal fragment or on the maxilla.

Occiput

The occiput of *Bathignathus poikilops* is represented by a small section of the left-hand side of the skull, namely the proximal portions of the paroccipital process of the tabular and supraoccipital process of the postparietal. These processes border the left post-temporal fenestra which, although incomplete ventrally, appears to have been small and subcircular in shape in the usual brachyopid fashion. The occiput is not sufficiently preserved to determine the slope and distance of the occipital condyles away from the skull table. In the reconstruction (Figure 3) this has been drawn to resemble that of *Bathignathus watsoni* in having a relatively short posterior projection, unlike the extreme posterior projection of *Batrachosuchus browni*.

Mandible

(Figure 4)

The mandible of *Bathignathus poikilops* is arguably the most complete and well-preserved brachyopid mandibular ramus known, alongside the recently described (but not named) brachyopid mandible (QM F14483) from the Early Triassic of Australia (Damiani & Warren 1996). The mandible is unusual for a brachyopid in that anteriorly the ramus is relatively tall

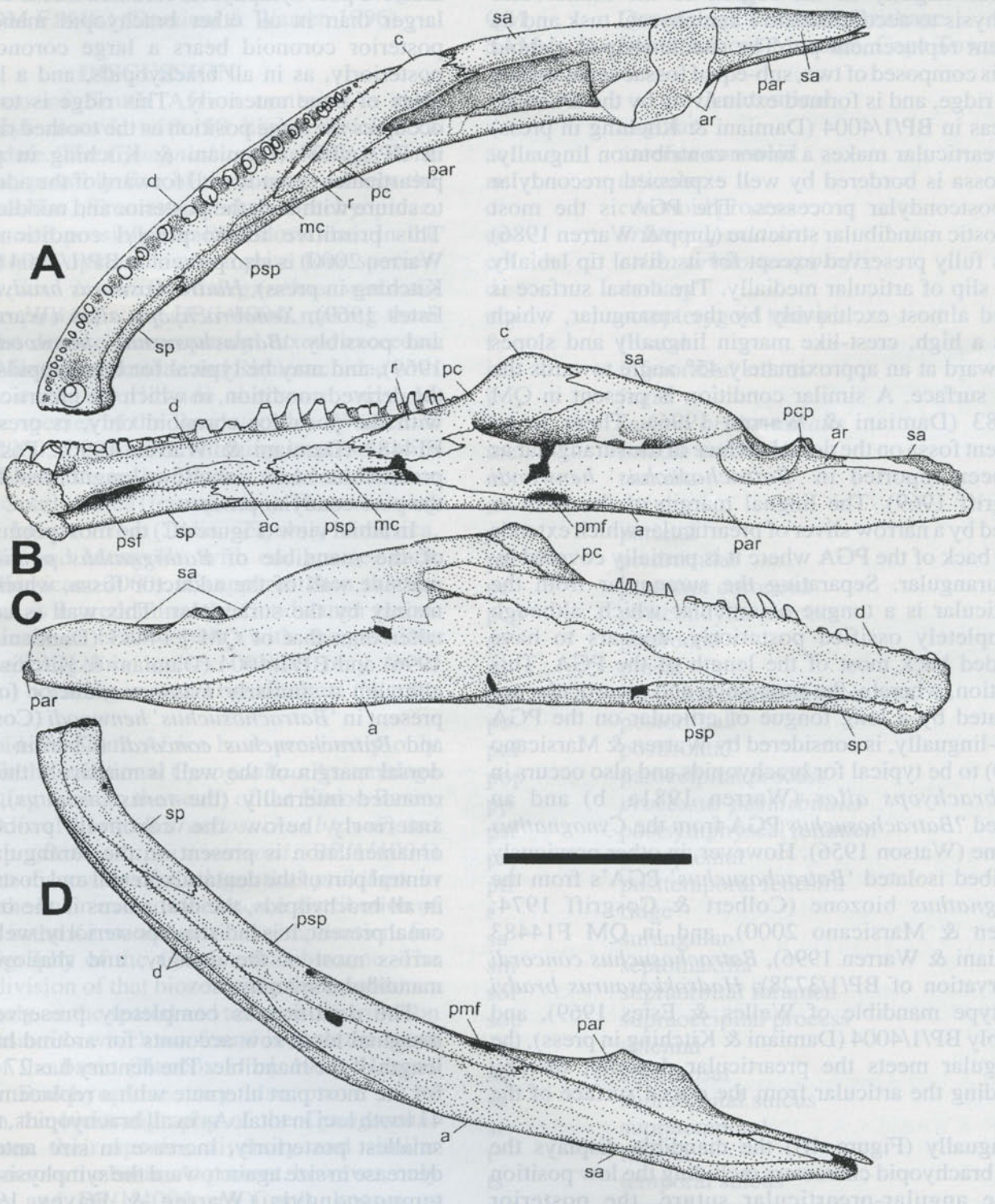

Figure 4. *Bathignathus poikilops sp. nov.* (BP/1/5883), interpretive drawings of the right mandible in A, dorsal, B, lingual, C, labial and D, ventral views. Scale bar equals 50 mm.

and narrow, whereas typically in brachyopids the mandible is low and broad anteriorly (Warren 1981a). The glenoid fossa is positioned slightly below the level of the dentary tooth row. As in all brachyopids, the ventral margin of the mandible is straight and the tooth row is short and comprises less than half the total mandibular length. The total length of the mandible from the front of the mandibular symphysis to the tip of the post-glenoid area (PGA) is 266 mm; the PGA measures 52 mm from the post-condylar process to its tip.

In dorsal view (Figure 4A), the dentary forms a convex shelf medial to the tooth row. This shelf expands slightly in the region of the mandibular symphysis to accommodate a symphyseal tusk and its adjacent replacement pit. The saddle-shaped glenoid fossa is composed of two, sub-equal fossae separated by a low ridge, and is formed exclusively by the articular, whereas in BP/1/4004 (Damiani & Kitching in press) the prearticular makes a minor contribution lingually. The fossa is bordered by well expressed precondylar and postcondylar processes. The PGA is the most diagnostic mandibular structure (Jupp & Warren 1986) and is fully preserved except for its distal tip labially and a slip of articular medially. The dorsal surface is formed almost exclusively by the surangular, which forms a high, crest-like margin lingually and slopes downward at an approximately 45° angle towards the labial surface. A similar condition is present in QM F14483 (Damiani & Warren 1996). There is no apparent fossa on the dorsal surface of the surangular as has been reported in *'Batrachosuchus' henwoodi* (Cosgriff 1969). The lingual margin of the PGA is formed by a narrow sliver of prearticular which extends to the back of the PGA where it is partially covered by the surangular. Separating the surangular from the prearticular is a tongue of articular which, although incompletely ossified posteriorly, appears to have extended back most of the length of the PGA. This condition, whereby the surangular and prearticular are separated by a long tongue of articular on the PGA dorso-lingually, is considered by Warren & Marsicano (2000) to be typical for brachyopids and also occurs in *Xenobrachyops allos* (Warren 1981a, b) and an isolated ?*Batrachosuchus* PGA from the *Cynognathus* biozone (Watson 1956). However, in other previously described isolated *'Batrachosuchus'* PGA's from the *Cynognathus* biozone (Colbert & Cosgriff 1974; Warren & Marsicano 2000), and in QM F14483 (Damiani & Warren 1996), *Batrachosuchus concordi* (observation of BP/1/3728), *Hadrokkosaurus bradyi* (holotype mandible of Welles & Estes 1969), and possibly BP/1/4004 (Damiani & Kitching in press), the surangular meets the prearticular dorsally, thereby excluding the articular from the dorsal surface of the PGA.

Lingually (Figure 4B) the mandible displays the usual brachyopid characters including the low position of the angular-prearticular suture, the posterior extension of the prearticular onto the PGA, the absence of a chordatympanic foramen, the absence of an anterior meckelian foramen, and the small posterior meckelian foramen positioned low on the lingual surface (Cosgriff 1974; Warren 1981a, b; Jupp & Warren 1986). However, the latter is distinctive in being bordered only by the prearticular and postsplenial, with no contribution from the angular as occurs in all other known brachyopid mandibles. Anteriorly the splenial forms the lower margin of the mandibular symphysis, as in QM F14483 (Damiani & Warren 1996) but not BP/1/4004 (Damiani & Kitching in press), in which the symphysis is formed entirely by the dentary. The mandibular symphysis shows a massive post-symphyseal foramen that is considerably larger than in all other brachyopid mandibles. The posterior coronoid bears a large coronoid process posteriorly, as in all brachyopids, and a longitudinal ridge of bone anteriorly. This ridge is toothless and occupies the same position as the toothed ridge present in BP/1/4004 (Damiani & Kitching in press). The prearticular extends well forward of the adductor fossa to suture with both the posterior and middle coronoids. This primitive temnospondyl condition (Yates & Warren 2000) is also present in BP/1/4004 (Damiani & Kitching in press), *Hadrokkosaurus bradyi* (Welles & Estes 1969), *Xenobrachyops allos* (Warren 1981a), and possibly *'Batrachosuchus' henwoodi* (Cosgriff 1969), and may be typical for brachyopids. However, the derived condition, in which the prearticular sutures with the posterior coronoid only, is present in QM F14483 (Damiani & Warren 1996). Posteriorly the prearticular bears a shallow, longitudinal fossa below the post-condylar process.

In labial view (Figure 4C) the most prominent aspect of the mandible of *Bathignathus poikilops* is the massive wall of the adductor fossa, which is formed mainly by the surangular. This wall is considerably taller than that of QM F14483 (Damiani & Warren 1996) and BP/1/4004 (Damiani & Kitching in press), although a similarly massive adductor fossa wall is present in *'Batrachosuchus' henwoodi* (Cosgriff 1969) and *Batrachosuchus concordi* (Chernin 1977). The dorsal margin of the wall is massively thickened and rounded internally (the *torus arcuatus*), especially anteriorly below the coronoid process. Light ornamentation is present on the surangular, angular, ventral part of the dentary, splenial and postsplenial. As in all brachyopids, the oral sulcus is the only sensory canal present. It is indistinct posteriorly, well impressed across most of the dentary, and shallows near the mandibular symphysis.

The dentition is completely preserved and the marginal tooth row accounts for around half the total length of the mandible. The dentary has 27 teeth which for the most part alternate with a replacement pit, and 41 tooth loci in total. As in all brachyopids, the teeth are smallest posteriorly, increase in size anteriorly, and decrease in size again toward the symphysis. As in most temnospondyls (Warren & Davey 1992) tooth implantation is clearly pleurodont, and individual teeth

are variously sub-circular to elliptical at their base and possess distinctive pulp cavities. The larger teeth are clearly xiphoid; that is, their upper parts are recurved and possess cutting edges (carinae) on their anterior and posterior edges. This is the usual condition in brachyopids (Warren & Davey 1992). The dentary tusk is round in cross-section at its base and only moderately larger than the largest marginal tooth. There are neither post-symphyseal teeth nor teeth on any of the coronoids. This contrasts with all other brachyopids which possess teeth on at least the posterior coronoid (Warren & Davey 1992), including *Hadrokkosaurus bradyi* (Welles & Estes 1969), *Xenobrachyops allos* (Warren 1981b), BP/1/4004 (Damiani & Kitching in press) and QM F14483 (Damiani & Warren 1996).

DISCUSSION

The Karoo of South Africa contains a rich temnospondyl record, with 10 higher-level taxa recorded to date. The *Cynognathus* Assemblage Zone contains four, possibly five of these taxa, namely the Mastodonsauridae, Trematosauridae, Brachyopidae, Laidleriidae, and possibly the Rhytidosteidae. In the Karoo the Brachyopidae now comprise four species, *Batrachosuchus browni*, *Bathignathus watsoni*, *Bathignathus poikilops* and BP/1/4004, making them the third most diverse temnospondyl taxon, exceeded only by the Mastodonsauridae and Rhinesuchidae with six species each. Worldwide there are only 15 determinable species of the Brachyopidae (Warren & Marsicano 2000; Damiani & Kitching in press), with the highest diversities in the Triassic of Australia (five species) and South Africa (four species). The remaining species are known from India, Zambia, America, China, Russia and Mongolia, with one species each (Warren & Marsicano 2000). It is apparent then, that the Brachyopidae is a predominantly Gondwanan taxon, the only Laurasian brachyopids (with the possible exception of *Vigilius wellesi* which may be a dvinosaurian) occuring in post-Triassic strata (Warren *et al.* 1997).

Brachyopids in South Africa have previously only been found in the traditional *Cynognathus* Assemblage Zone collecting areas in the south of the Karoo Basin, around the Aliwal North (*Batrachosuchus browni*) and Burgersdorp (*Bathignathus watsoni*, BP/1/4004) districts. The discovery of *Bathignathus poikilops* in the north of the basin extends the known distribution of brachyopids in the Karoo and may have implications for the biostratigraphy of the *Cynognathus* biozone. The current subdivision of that biozone into three subzones is based largely on the spatial and temporal distribution of mastodonsaurids which are found in both the south and north of the basin (Hancox *et al.* 1995; Hancox 2000). The Brachyopidae may also prove to be important in the biostratigraphy of the *Cynognathus* biozone given their species diversity and similar distribution across the basin. At present, however, only *B. poikilops* and BP/1/4004 are firmly known as pertaining to the lower and middle parts of the *Cynognathus* biozone, respectively, as both *B. browni* and *B. watsoni* are of uncertain provenance. Further collecting, especially in the newly discovered and as yet incompletely known faunas in the north (Welman et al. 1991; Neveling 2002) and extreme south of the basin (Hancox 1998, 2000), should help to refine the biostratigraphy and age correlation of the *Cynognathus* Assemblage Zone.

ABBREVIATIONS

Institutional

BMNH	Natural History Museum, London
BP	Bernard Price Institute for Palaeontological Research, Johannesburg
QM	Queensland Museum, Brisbane
SAM	South African Museum, Cape Town

Anatomical

a	angular
ac	anterior coronoid
ar	articular
c	coronoid process
cc	*crista capsularis*
cot	*crista orbito-temporalis*
d	dentary
etp	ectopterygoid tusk-pit
f	frontal
is	infraorbital sulcus
j	jugal
lon	*lamina orbito-nasalis*
mc	middle coronoid
mx	maxilla
n	nasal
p	parietal
par	prearticular
pc	posterior coronoid
pcp	postcondylar process
pf	prefrontal
pi	pineal
pmf	posterior meckelian foramen
po	postorbital
pof	postfrontal
pop	paroccipital process
pp	*processus postorbitalis*
psf	postsymphyseal foramen
psp	postsplenial
ptf	posttemporal fenestra
r	ridge
sa	surangular
sm	septomaxilla
sof	supraorbital foramen
sop	supraoccipital process
sp	splenial
sq	squamosal
ss	supraorbital sulcus
st	supratemporal
t	tabular
ts	temporal sulcus
vpt	ventral process on tabular

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