

https://dspace.org/

A review of the South African temnospondyl amphibian record

Damiani, RJ; Rubidge, BS

2003-12
Bernard Price Institute for Palaeontological Research
http://hdl.handle.net10539/13304

Downloaded from a DSpace repository. https://dspace.org/

A review of the South African temnospondyl amphibian record

R.J. Damiani* **& B.S. Rubidge**

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa

Received 14 February 2002. Accepted 30 September 2003

The Karoo of South Africa preserves a near-unbroken sequence of sedimentary rocks and associated vertebrate fauna from the Late Carboniferous to the Middle Jurassic periods. These rocks host a rich temnospondyl amphibian record from the Late Permian to the Early Jurassic. This record is amongst the most diverse temnospondyl record in the world and comprises 10 higher-level taxa, most of which occur in the Triassic part of the sequence and which is dominated by members of the Stereospondyli, with lesser representation by two Palaeozoic lineages. This paper presents a synthesis of the South African temnospondyl amphibian record and highlights the most recent advances in their taxonomy and biostratigraphic placement.

Keywords: South Africa, Karoo, temnospondyls, stereospondyls.

INTRODUCTION

The Karoo Basin of South Africa preserves a continuous sequence of sedimentary rocks from the Late Carboniferous through to the Middle Jurassic periods (Smith 1990). Within this thick succession, the Permo-Triassic Beaufort Group and overlying Triassic-Jurassic Stormberg Group preserve a rich fossil biota that documents the evolution of terrestrial life during the late Palaeozoic and early to middle Mesozoic eras. These rocks are world renowned primarily for their therapsid ('mammal-like reptile') fauna, the diversity and abundance of which have allowed for the biostratigraphic subdivision of the sequence (Kitching 1977; Kitching & Raath 1984; Rubidge 1995). Less well known amongst Karoo fossil vertebrates are the temnospondyl amphibians, which are surpassed only by therapsids in terms of diversity and abundance.

The Temnospondyli was the largest, most diverse and most successful group of fossil amphibians, ranging in time from the Early Carboniferous to the Early Cretaceous (Milner 1990). Temnospondyls were superficially salamander-like in appearance with a total body length that varied from below 1 m to 6 m or more, most being above 1 m. They have also been widely linked to the origin of some or all of the modern lissamphibian groups (e.g. Milner 1988; Bolt 1991; Trueb & Cloutier 1991). Temnospondyls have been recovered from all continents and are near-ubiquitous components of non-marine sedimentary rocks of Permian and Triassic age. This abundance has led to their playing an important and sometimes critical role in local biostratigraphy and global correlation of non-marine strata of Triassic age (e.g. Hancox *et al.* 1995; Ivakhnenko *et al.* 1997; Ochev & Shishkin 1989; Lucas 1998).

In the Karoo the temnospondyl fauna is dominated by members of the great Mesozoic radiation of temnospondyls known as the Stereospondyli (Milner 1990; Yates & Warren 2000), with members of the Palaeozoic lineages Dvinosauria and Dissorophoidea making up the non-stereospondyl component. The Permo-Triassic Beaufort Group contains all but one of the higher-level temnospondyl taxa known from the Karoo, with most of these occurring in the Triassic part of the Group. The overlying Triassic-Jurassic 'Stormberg Group' has received far less attention palaeontologically, a fact reflected in the considerably lower diversity of tetrapods, including temnospondyls (Kitching & Raath 1984). Despite this overall rich temnospondyl record, relatively little research has been directed towards Karoo temnospondyls. In recent years, however, there has been a resurgence of interest in South African temnospondyls, especially in taxonomic studies (see review below), their role in interpreting the basin development of the Karoo (Hancox & Rubidge 1997; Hancox 1998), and in local biostratigraphy and correlation of non-marine tetrapod faunas (Hancox *et al.* 1995; Shishkin *et al.* 1995; Lucas 1998; Damiani 1999; Hancox *et al.* 2000; Shishkin 2000).

The only previous review of Karoo temnospondyls was that of Kitching (1978), a paper which was concerned primarily with documenting the total numbers and stratigraphic distribution of the temnospondyl fauna of the Beaufort Group. Since then, a significant number of new temnospondyl taxa have been described, additional information has been obtained through redescriptions of older material, and stratigraphic and biostratigraphic advances have been made. The aim of this paper is to summarize the taxonomy as well as stratigraphic occurrence of all known temnospondyls from the Karoo. It is not the intention here to critically reassess the relationships of each temnospondyl species discussed, although we provide a brief summary of the taxonomic history of those species whose relationships have been controversial. In the review below, higher-level taxa are arranged in alphabetical order, whereas individual species within each higher-level taxon are listed in chronological order of description. Synonymy lists include only those references in which a change in a taxon name has occurred. Note that the relationships of the Brachyopidae and Chigutisauridae

*Author for correspondence. E-mail: damianir@geosciences.wits.ac.za

within the Temnospondyli remain controversial (Shishkin 1991; Schoch & Milner 2000; Yates & Warren 2000; Damiani & Kitching 2003), and are here listed under the Stereospondyli merely for convenience. We precede our review with a brief outline of the Palaeozoic and Mesozoic geology of the Karoo in order to provide the necessary stratigraphic and biostratigraphic framework. Photographs of the skulls of Karoo temnospondyls, in dorsal view, are presented in Figs 1–3. A chart illustrating the biostratigraphic distribution of Beaufort Group temnospondyls is presented elsewhere (Damiani, in press), and is not repeated here.

Institutional abbreviations in the text are as follows: AM, Albany Museum, Grahamstown; BMNH, Natural History Museum, London; BP, Bernard Price Institute for Palaeontological Research, Johannesburg; BSP, Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich; CGP, Council for Geoscience, Pretoria; MA, Museum Africa, Johannesburg; FMNH, Field Museum of Natural History, Chicago; GPIT, Institut und Museum für Geologie und Paläontologie, Tübingen; MGM, MacGregor Museum, Kimberley; NM, National Museum, Bloemfontein; RC, Rubidge Collection, Wellwood, Graaff-Reinet; SAM, South African Museum, Cape Town; TM, Transvaal Museum, Pretoria; UCMP, University of California Museum of Paleontology, Berkeley; UMZC, University Museum of Zoology, Cambridge.

GEOLOGICAL SETTING

The Karoo Basin of South Africa preserves a 12 km thick succession of mainly sedimentary rocks that accumulated in a retroarc foreland basin during the Late Carboniferous to Early Jurassic in southwestern Gondwana (Johnson *et al.* 1997; Catuneanu *et al.* 1998). These rocks reflect changing depositional environments including glacial, deep marine, deltaic, fluvial and aeolian (Smith 1990), and have yielded a diverse fossil biota consisting of plants, vertebrates, invertebrates, and trace fossils (Hancox & Rubidge 1997).

Lithostratigraphically the Karoo Supergroup is subdivided into five main groups. These are, in ascending stratigraphic order, the Dwyka, Ecca, Beaufort, 'Stormberg' and Drakensberg groups, broadly representing deposition in glacial (Dwyka), marine (Ecca) and terrestrial (Beaufort and Stormberg) environments (Smith 1990). This sedimentary sequence is capped by the Drakensberg volcanics which terminated sedimentation in the basin in the Middle Jurassic (Smith 1990). Vertebrate fossils in this sequence are known from the Ecca, Beaufort and 'Stormberg' groups.

The Early to Late Permian-aged Ecca Group consists of 16 different formations in the various parts of the basin (Johnson *et al.* 1997). In terms of vertebrate fossils, actinopterygian fish are common in several of these formations. The mesosaurid reptiles *Mesosaurus* and *Stereosternum* are the only tetrapods from the Ecca (Oelofsen 1981, 1987; Modesto 1996), and are confined to the Early Permian Whitehill Formation, a white-weathering, black carbonaceous shale considered to have been deposited in a deep-water, anoxic environment (Oelofsen 1987; Catuneanu *et al.* 1998). *Mesosaurus* and *Stereosternum* are of particular importance as representing the oldest known amniotes from Gondwana.

The Beaufort Group conformably overlies the Ecca Group and the lithological contact between these groups is thought to coincide with the position of the 'palaeo-shoreline' (Rubidge *et al.* 2000). Its 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 Beaufort Group preserves a complete Late Permian to early Middle Triassic (Rubidge 1995) sedimentary sequence and associated vertebrate fauna, and has long been recognized as the global standard for the non-marine Permo-Triassic (Romer 1975; Cosgriff 1984; Lucas 1998). This 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 & Smith 1979; Rubidge 1995).

The current biostratigraphic scheme of the Beaufort Group consists of eight assemblage zones (Rubidge 1995); these have been broadly linked to the lithostratigraphy which comprises many formational names in the various parts of the basin (Keyser & Smith 1979; Rubidge 1995). These biozones are, in ascending order from oldest to youngest, the *Eodicynodon, Tapinocephalus, Pristerognathus, Tropidostoma, Cistecephalus, Dicynodon, Lystrosaurus* and *Cynognathus* Assemblage zones. The first six of these biozones are of Late Permian age (Rubidge 1995), the *Lystrosaurus* Assemblage Zone is broadly Early Triassic in age (Groenewald & Kitching 1995; Hancox 2000), and the *Cynognathus* Assemblage Zone is of Early-Middle Triassic age (Hancox 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 & Shishkin 1989) age, it is now considered to straddle the Early-Middle Triassic boundary. The Permo-Triassic boundary in the Karoo Basin is currently held to occur within the lowest part of the *Lystrosaurus* Assemblage Zone, and is defined by the last appearance of the dicynodont *Dicynodon* (Smith 1995). At present there are no formal subdivisions of the various Beaufort biozones although the *Cynognathus* Assemblage Zone has been subdivided into a lower 'A' zone (upper Olenekian), a middle 'B' zone (early Anisian), and an upper 'C' zone (late Anisian) (Hancox *et al.* 1995; Shishkin *et al.* 1995; Hancox & Rubidge 1997).

The 'Stormberg Group' unconformably overlies the Beaufort Group and is separated from it by a time gap representing the entire late Middle Triassic (Ladinian) (Hancox 2000). The 'Stormberg Group' consists of, in ascending stratigraphic order, the Molteno, Elliot and Clarens formations. The Molteno Formation is of Late Triassic (possibly Carnian) age (Hancox 2000); it hosts a diverse insect and plant assemblage, but as of yet the only

vertebrate body fossils are of fish (Anderson & Anderson 1984). The overlying Lower Elliot Formation is regarded by some workers to be a coeval, distal equivalent of the uppermost Molteno Formation (Cairncross *et al.* 1995; Anderson *et al.* 1998). It hosts a relatively meagre vertebrate fauna (Anderson *et al.* 1998) that has been assigned to the *Euskelosaurus* Range Zone (Kitching & Raath 1984) and used to support a Late Triassic age (Kitching & Raath 1984; Olsen & Galton 1984). The middle and upper parts of the Elliot Formation host a more diverse and abundant vertebrate fauna (Kitching & Raath 1984; Anderson *et al.* 1998) that, along with the lower part of the overlying Clarens Formation, has been assigned to the *Massospondylus* Range Zone (Kitching & Raath 1984) and used to support an Early Jurassic age (Smith & Kitching 1997; Anderson *et al.* 1998). Finally, the Clarens Formation hosts a meagre vertebrate record consisting primarily of elements of the underlying Upper Elliot Formation (Kitching & Raath 1984), and is of Early-Middle Jurassic age. Although vertebrate fossils are considerably less abundant in the Stormberg than in the Beaufort Group, this is compensated for by the presence of some of the earliest dinosaurs and mammals in the world (Kitching & Raath 1984). The Elliot Formation also preserves the last known temnospondyls from the Karoo (Warren & Damiani 1999).

REVIEW OF SOUTH AFRICAN TEMNOSPONDYLS

Temnospondyli Zittel 1887–1890
Dissorophoidea Boulenger 1902
Amphibamidae Moodie 1910

Micropholis stowii Huxley 1859, Fig. 1A
Petrophryne granulata Owen 1876a
Micropholis granulata Lydekker 1890b

Holotype. BMNH R4382, a skull, partially preserved as an internal mould, with attached lower jaw and partial pectoral girdle.

Locality and horizon. Given by Huxley (1859) as the 'foot of the Rhenosterberg', and by Watson (1913) as 'Rhenosterberg (north-west of New Bethesda), District Graaff-Reinet, Cape Colony', although the Rhenosterberg Range lies mainly in the southwest of the adjacent Middelburg District; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. BMNH R510, the holotype skull of '*Petrophryne granulata*' Owen (Watson 1913); BMNH R510a, a skull (Watson 1913); BSP 1934 VIII 42 and BSP 1934 VIII 43, three and five near-complete skeletons in sandstone nodules, respectively (Broili & Schröder 1937a). All specimens from the farm Donnybrook, Queenstown District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. The somewhat enigmatic small temnospondyl *Micropholis stowii* was initially placed in its own higher-level taxon, the Micropholidae (Watson 1919), which was accepted by most subsequent workers (Haughton 1925; Kuhn 1933; Romer 1947; Huene 1956; Milner 1990; Warren & Hutchinson 1990). However, it is also widely referred to the Dissorophidae (Carroll & Winer 1977; Cosgriff 1984). Most recently, Daly (1994) recognized an assemblage of primitive dissorophoids, including *M. stowii,* which she transferred to the Amphibamidae. *M. stowii* is of particular importance as representing the last surviving member of the dissorophoid temnospondyls. The species was redescribed by Boy (1985) on the basis of Broili & Schröder's (1937a) material, and new material is currently under description by Schoch & Rubidge. Van Heerden (1974) described a supposed skin impression of the reptile *Procolophon,* which was reinterpreted by Gow (1977) as the cast of a temnospondyl skull roof. Schoch & Milner (2000) attributed that specimen, NM QR1597, to *Lydekkerina,* but the presence of nodular ornament, large orbits, and a large otic notch (*cf.* Gow 1977) is identical to *M. stowii* and unlike *Lydekkerina.*

Dvinosauria Yates & Warren 2000
Tupilakosauridae Kuhn 1960

Thabanchuia oomie Warren 1999, Fig. 1B

Holotype. UCMP 42780, a near-complete skull with attached mandibular rami, and associated postcranial elements.

Locality and horizon. UCMP locality V4744, near Thaba N'chu, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. UCMP 42777, UCMP 42781, partial skulls and associated postcranial elements, and UCMP 42778, a string of articulated vertebrae with some ribs (Warren 1999); locality and horizon as for holotype.

Remarks. Thabanchuia oomie represents the fourth member of the rare higher-level taxon Tupilakosauridae, alongside *Tupilakosaurus heilmani* from the Early Triassic of East Greenland (Nielson 1954), *Tupilakosaurus wetlugensis* from the Early Triassic of Russia (Shishkin 1961), and possibly *Kourerpeton bradyi* from the ?Late Permian of North America (Olsen & Lammers 1976; Warren 1999). The Tupilakosauridae represent relict survivors of the Palaeozoic Dvinosauria (Warren 1999; Yates & Warren 2000).

Stereospondyli Zittel 1887–1890
Brachyopidae Lydekker 1885

Batrachosuchus browni Broom 1903, Fig. 1C

Holotype. SAM-PK-5868, a near-complete skull.

Locality and horizon. An unknown locality in the Aliwal North District, Eastern Cape Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Aliwal North District.

Referred material. None.

Remarks. The holotype and only known specimen was collected by Mr Alfred Brown of Aliwal North, and described in an exceedingly brief note by Broom. An attempt was made to trace the type locality from Brown's extensive personal diaries held at the South African Museum, but there was nothing on record about its collection. Additional descriptions of *Batrachosuchus browni* have been provided by Haughton (1925), Watson (1956), Welles & Estes (1969) and Chernin (1977).

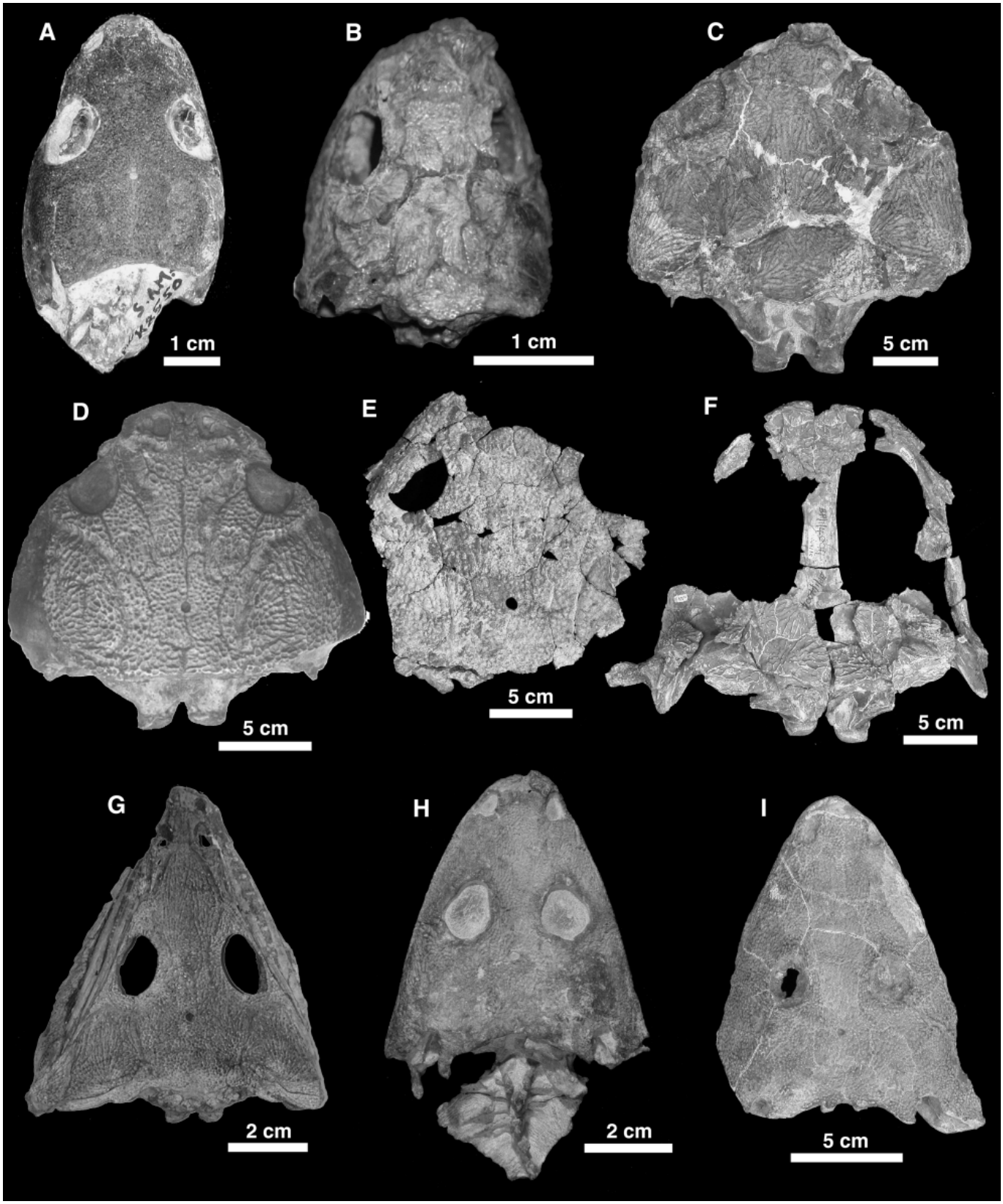


Figure 1. Photographs (in dorsal view) of the skulls of South African temnospondyls. **A**, *Micropholis stowii,* SAM-PK-K8550; **B**, *Thabanchuia oomie,* holotype, UCMP 42780; **C**, *Batrachosuchus browni,* holotype, SAM-PK-5868; **D**, *Bathignathus watsoni,* holotype, BMNH R3589; **E**, *Bathignathus poikilops,* holotype, BP/1/5790; **F**, *Vanastega plurimidens,* holotype, BP/1/4004; **G**, *Laidleria gracilis,* holotype, AM 4313; **H**, *Lydekkerina huxleyi,* holotype, BMNH R507; **I**, *Eolydekkerina magna,* holotype, BP/1/5079.

***Batrachosuchus* sp.**

Material. UMZC T194, a mandibular fragment, and UMZC T193, an atlas (Watson 1956). UCMP 42856 and UCMP 80859–60, assorted cranial and postcranial remains (Welles & Estes 1969), now renumbered as follows: UCMP 42856, cranial and vertebral remains; UCMP 140568–69, 140571–72, 140575–78 and 140586, skull fragments; UCMP 140587–92, mandibular fragments; UCMP 80857–58,

140580, 140584, 140570, 140573–74, 140583, 140585 and 80859–60, postcranial remains.

Locality and horizon. UMZC material from the farm Luiperkop (not 'Luiper Kop' of Watson (1956) or 'Luiperdskop' of Kitching (1963)), Burgersdorp District, Eastern Cape Province (not 'Orange Free State' of Warren & Marsicano (2000)); *Cynognathus* Assemblage Zone, Early-Middle Triassic. UCMP material from the farm Slootkraal, Rouxville District, Free State Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian. Note that Welles & Estes (1969) ascribe the UCMP material to the farm Bethel; however, the locality from which the material was recovered actually belongs to the farm Slootkraal (Renaut, pers. comm.).

Remarks. Further descriptions of some of the UCMP material have been provided by Colbert & Cosgriff (1974) and Warren & Marsicano (2000). Although this material has been referred to *Batrachosuchus,* there seems no reason why some of this material should not pertain to another brachyopid genus from the Karoo.

Bathignathus watsoni (Haughton) Damiani & Jeannot 2002, Fig. 1D

Batrachosuchus sp. Watson 1919

Batrachosuchus watsoni Haughton 1925

Holotype. BMNH R3589, a near-complete skull.

Locality and horizon. Unknown, but presumed by Watson (1956) to have come from the Burgersdorp District, Eastern Cape Province, and thus from the *Cynognathus* Assemblage Zone which is widely exposed in this district.

Referred material. None.

Remarks. Redescribed by Watson (1956) and Welles & Estes (1969), who separated the species from *Batrachosuchus browni* largely on skull proportions. Chernin (1977) listed further morphological differences and, following Welles & Estes (1969), suggested that *'Batrachosuchus' watsoni* may be sufficiently distinct from *B. browni* to warrant generic separation. However, Warren & Marsicano (2000) suggested that the species may be conspecific. Damiani & Jeannot (2002) listed further morphological differences and erected a new genus, *Bathignathus,* for *'B.' watsoni.*

Bathignathus poikilops Damiani & Jeannot 2002, Fig. 1E

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

Locality and horizon. Farm Driefontein, Paul Roux District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Referred material. BP/1/5883, a complete right mandibular ramus (Damiani & Jeannot 2002); locality and horizon as for holotype.

Remarks. This brachyopid shows phenetic similarities to both *Batrachosuchus browni* and *Bathignathus ('Batrachosuchus') watsoni,* but was argued (Damiani & Jeannot 2002) to show closest affinities with the latter.

Vanastega plurimidens Damiani & Kitching 2003, Fig. 1F

Holotype. BP/1/4004, a partial skull and associated cranial fragments, and a near-complete left mandibular ramus.

Paratype. BP/1/5831, a partial left mandibular ramus.

Locality and horizon. Farm Nooitgedacht, Burgersdorp District, Eastern Cape Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian.

Referred material. None.

Remarks. A brachyopid remarkable for apparently being most closely related to the North American *Vigilius wellesi* (Welles & Estes 1969; Warren & Marsicano 2000), a species suggested (Shishkin 1991; Warren & Marsicano 2000) to be a dvinosaurian.

Chigutisauridae Rusconi 1949

cf. *Siderops* sp. Warren & Damiani 1999

Material. BP/1/5092, a partial skull with attached partial mandibular rami.

Locality and horizon. Farm Vastrap, Ladybrand District, Free State Province; Upper Elliot Formation, Early Jurassic.

Remarks. This and the material described below as Chigutisauridae indet. from the Late Triassic-Early Jurassic Elliot Formation represent the last known temnospondyls from the Karoo and the undoubted post-Triassic stereospondyls from Africa. Significantly, all well-known post-Triassic stereospondyl remains from Gondwana appear to be chigutisaurid, including the Elliot material. This material had previously been mentioned by Kitching & Raath (1984), Olsen & Galton (1984) and Hopson (1984), with the Lower Elliot material being referred to as capitosaurid and the Upper Elliot material as brachyopid. All of this material was examined by Warren & Damiani (1999) and found to be chigutisaurid.

Chigutisauridae indet.

Material. BP/1/4750, fragmentary cranial and postcranial remains from the farm Friesland West, Bethlehem District, Free State Province; Lower Elliot Formation, Late Triassic (Warren & Damiani 1999).

BP/1/5111, a partial left mandible with attached skull remains, articulated and disarticulated vertebrae, detached partial ribs, and a fragment of interclavicle from the farm Broken Slopes (an annexe of the farm Vastrap), Ladybrand District, Free State Province; Upper Elliot Formation, Early Jurassic (Warren & Damiani 1999).

BP/1/5252, partial left and right mandibular rami with associated cranial material from the farm Hollywood, Lady Grey District, Eastern Cape Province; Lower Elliot Formation, Late Triassic (Warren & Damiani 1999).

BP/1/5406, fragments of a skull with attached mandibular fragments, vertebral elements and a partial femur from the farm Vastrap, Ladybrand District, Free State Province; Upper Elliot Formation, Early Jurassic (Warren & Damiani 1999).

Laidleriidae Kitching 1957

Laidleria gracilis Kitching 1957, Fig. 1G

Holotype. AM 4313, an articulated skeleton comprising a complete skull with attached partial lower jaw, and presacral postcranial skeleton.

Locality and horizon. Elucwecwe, Engcobo District, East-

ern Cape Province; *Cynognathus* Assemblage Zone, Early-Middle Triassic.

Referred material. None.

Remarks. Kitching (1957) tentatively placed *Laidleria gracilis* in the Trematosauridae, but suggested that the species may in future be referred to a new 'family', the Laidleriidae. The species was retained in the monotypic Laidleriidae by some workers and considered closely related to the Rhytidosteidae (Cosgriff 1965; Warren 1998), but placed directly in the Rhytidosteidae by others (Warren & Black 1985; Milner 1990; Schoch & Milner 2000). Cosgriff & Zawiskie (1979) considered the Laidleriidae as *incertae sedis* within the Temnospondyli, while Yates & Warren (2000) allied *Laidleria* with the enigmatic Plagiosauridae. The holotype skull was redescribed in detail by Warren (1998).

Lydekkerinidae Watson 1919

Lydekkerina huxleyi (Lydekker) Broom 1915, Fig. 1H

Bothriceps huxleyi Lydekker 1889
Putterillia platyceps Broom 1930
Limnoiketes paludinatans Parrington 1948
Lydekkerina sp. Parrington 1948

Holotype. BMNH R507, a complete skull.

Locality and horizon. An unknown locality near Edenburg, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. BMNH R504–506, R508, cranial and postcranial remains in sandstone nodules (Lydekker 1890b); locality and horizon as for holotype. SAM-PK-3525, a partial skull (Haughton 1925); BSP 1934 VIII 44, three skulls with associated partial postcranial skeletons in a sandstone nodule (Broili & Schröder 1937b); UMZC T238, a skull and associated cervical vertebrae (Parrington 1948); a partial skull and associated postcrania described as *Lydekkerina* sp. by Parrington (1948); UMZC T214, the holotype (a skull and pectoral girdle) of *Limnoiketes paludinatans* Parrington (Shishkin *et al.* 1996); TM 168, TM 88, the holotype (a skull) and paratype (a dermal shoulder girdle and lower jaw), respectively, of *Putterillia platyceps* Broom (Shishkin *et al.* 1996). All material except for BMNH specimens are from the Harrismith Commonage, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. Watson (1912, 1919) provided a redescription of some of the British Museum material, while Shishkin *et al.* (1996) provide additional data based on specimens from the TM, BPI and NM. Despite a wealth of specimens, the ontogeny and morphological variation within *Lydekkerina huxleyi* has never been studied, and forms the basis of a current research project by A.M. Jeannot. This study will also determine if only one species of *Lydekkerina* is present, as is universally assumed.

Broomulus dutoiti (Broom) Romer 1947

Lydekkerina dutoiti Broom 1930

Holotype. MGM 4285, a poorly preserved skull with associated lower jaws and partial pectoral girdle.

Locality and horizon. Harrismith Commonage, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. None.

Remarks. Variously considered a valid species, indeterminate, or a junior synonym of *Lydekkerina huxleyi.* The species was redescribed following additional preparation by Shishkin *et al.* (1996) who confirmed its status as a valid taxon differing from *L. huxleyi* by a suite of characters.

Eolydekkerina magna Shishkin *et al.* 1996, Fig. 1I

Holotype. BP/1/5079, a near-complete skull.

Locality and horizon. Farm Fairydale, Bethulie District, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. None.

Mastodonsauridae Lydekker 1885 *sensu* Damiani 2001a

Xenotosuchus africanus (Broom) Morales & Shishkin 2002, Fig. 2A

Capitosaurus africanus Broom 1909 *nomen nudum*
Capitosaurus africanus (Broom) Haughton 1925
Parotosaurus africanus (Broom) Watson 1962
Parotosuchus africanus (Broom) Chernin 1978
Wellesaurus africanus (Broom) Damiani 2001a

Lectotype. SAM-PK-2360, the posterior half of a skull and a partial left mandible; designated type by Haughton (1925), since Broom (1909) did not designate a holotype.

Locality and horizon. Farm Vaalbank, Burgersdorp District, Eastern Cape Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian.

Referred material. SAM-PK-3008, a poorly preserved skull (Haughton 1925); farm Winaarsbaken, Burgersdorp District, Eastern Cape Province. UCMP 41286, a near-complete skull and lower jaws (Morales & Shishkin 2002); farm Matabele, Rouxville District, Free State Province. Both specimens from Subzone B of the *Cynognathus* Assemblage Zone; early Anisian.

Remarks. Welles & Cosgriff (1965) considered '*Capitosaurus' africanus* a *nomen 'vanum'* since Broom (1909) did not figure the skull and provided only a cursory description. Chernin (1978) figured and redescribed the lectotype and transferred the species to the catch-all genus *Parotosuchus.* Shishkin *et al.* (1995), Maryanska & Shishkin (1996) and Damiani (2001a) suggested that '*Parotosuchus' africanus* may be related to *Wellesaurus peabodyi* (Welles & Cosgriff 1965; Damiani 2001a), and Damiani (2001a) transferred '*P.' africanus* to *Wellesaurus.* Most recently, Morales & Shishkin (2002) described a new specimen of *W. africanus* and transferred the species to a new genus, *Xenotosuchus,* but conceded that the species showed closest affinities to 'stenotosaurids' (including *Wellesaurus*).

Parotosuchus haughtoni (Broili & Schröder) Chernin 1978, Fig. 2B

Capitosaurus haughtoni Broili & Schröder 1937c
Parotosaurus haughtoni (Broili & Schröder) Romer 1947
Karoosuchus haughtoni (Broili & Schröder) Ochev 1966

Holotype. BSP 1934 VIII 50, a fragmentary skull, apparently destroyed during World War II. *Neotype*:

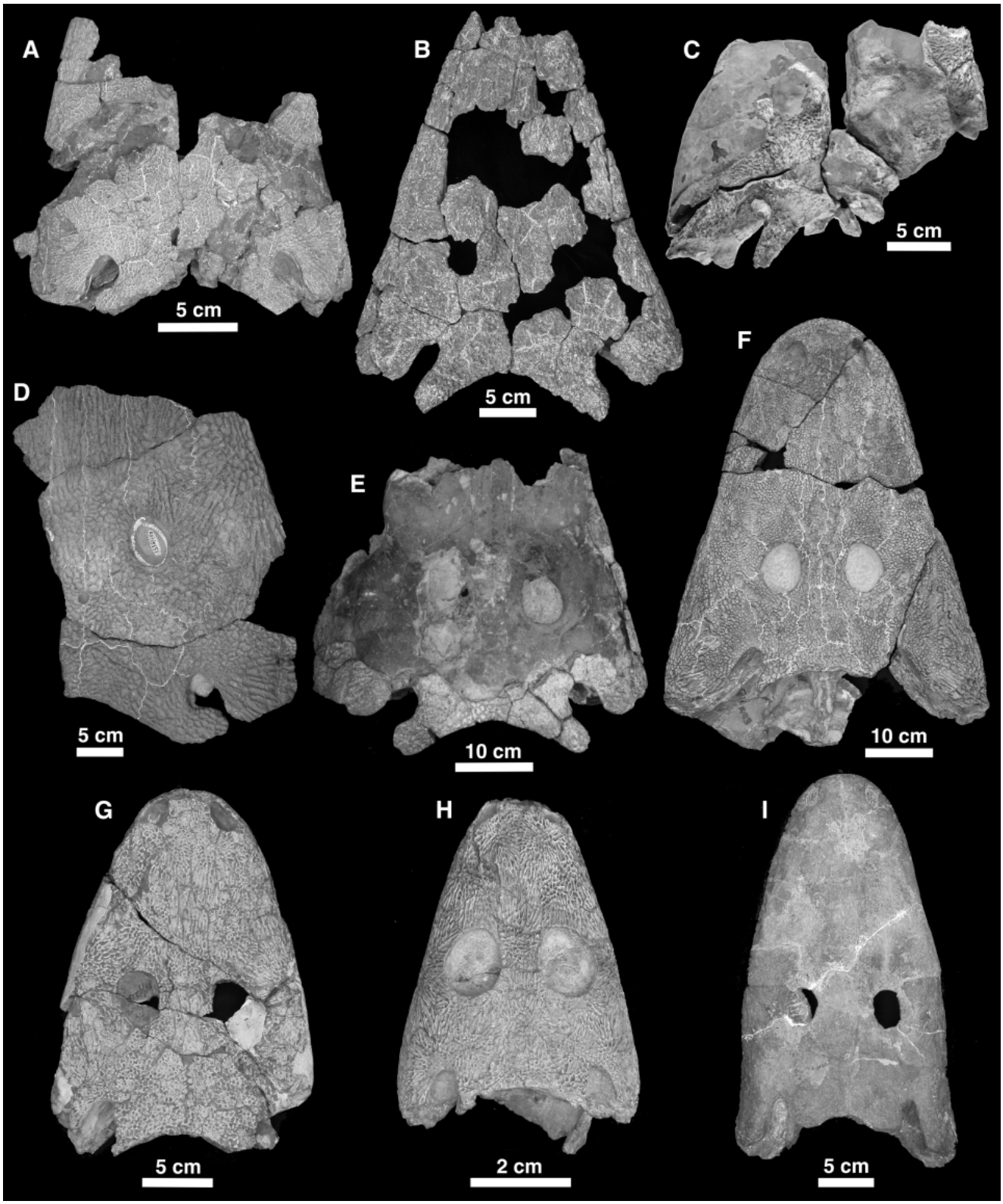


Figure 2. Photographs (in dorsal view) of the skulls of South African temnospondyls. **A**, *Xenotosuchus africanus,* holotype, SAM-PK-2360; **B**, *Parotosuchus haughtoni,* neotype, BP/1/5673; **C**, *Watsonisuchus magnus,* holotype, UMZC T173; **D**, *Paracyclotosaurus morganorum,* holotype, BP/1/5551; **E**, *Jammerbergia formops,* holotype, NM QR1436; **F**, *Uranocentrodon senekalensis,* referred specimen, NM QR1483; **G**, *Laccosaurus watsoni,* referred specimen, BP/1/213; **H**, *Broomistega putterilli,* referred specimen, BP/1/5058; **I**, *Rhinesuchoides tenuiceps,* holotype, FMNH UC 1519.

BP/1/5673, a partial skull and lower jaws, and associated intercentra (Damiani 2001b), designated neotype by Damiani (2001a).

Locality and horizon. Holotype: farm Kaaimansgat, Rouxville District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian. *Neotype:* Farm Driefontein, Paul Roux District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Referred material. None.

Remarks. This species was long known from the holotype specimen only and was usually referred by most

workers to the catch-all genus *Parotosuchus* (='*Capitosaurus*' and '*Parotosaurus*'), but placed in a new genus, *Karoosuchus,* by Ochev (1966). However, Damiani (1999, 2001b) described a new, near-complete specimen of *Parotosuchus haughtoni* which was made the neotype for the species (Damiani 2001a).

Watsonisuchus magnus (Watson) Ochev 1966, Fig. 2C
Wetlugasaurus sp. Watson 1919
Wetlugasaurus magnus Watson 1962
Parotosaurus sp. Welles & Cosgriff 1965
Parotosuchus sp. Warren 1980
Holotype. UMZC T173, the posterior half of a skull split into several sections, and fragments of a right mandible.
Locality and horizon. Farm Watford, Burgersdorp District, Eastern Cape Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.
Referred material. None.
Remarks. Considered by Watson (1919, 1962) to most closely resemble the Laurasian taxon *Wetlugasaurus* in general skull morphology, later transferred to the catch-all taxon '*Parotosaurus*' by Welles & Cosgriff (1965), but shown by Ochev (1966) to pertain neither to *Wetlugasaurus* or '*Parotosaurus*' (=*Parotosuchus*).

***Watsonisuchus* sp.** Damiani *et al.* 2001
Material. CGP 1/60, the posterior portion of a right mandible.
Locality and horizon. Farm T'Zamenkomst 120, Venterstad District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.
Remarks. This specimen represents the first undoubted record of a mastodonsaurid from the *Lystrosaurus* biozone.

Paracyclotosaurus morganorum Damiani & Hancox 2003, Fig. 2D
Parotosuchus morgani Hancox & Rubidge 1997, *nomen nudum*
Paracyclotosaurus Hancox *et al.* 2000
Holotype. BP/1/5551, the right posterior portion of a skull.
Locality and horizon. Farm Wilgerkloof, Sterkstroom District, Eastern Cape Province; Subzone C of the *Cynognathus* Assemblage Zone, late Anisian.
Referred material. None.

Jammerbergia formops Damiani & Hancox 2003, Fig. 2E
Holotype. NM QR1436, a partial skull.
Locality and horizon. Jammerberg, Wepener District, Free State Province; the horizon is presumably the *Cynognathus* Assemblage Zone (see discussion in Damiani & Hancox 2003).
Referred material. None.

Mastodonsauridae indet.

Cyclotosaurus albertyni Broom 1904, *nomen dubium*
Holotype. SAM-PK-K1876, fragments of a skull roof.
Locality and horizon. An unknown locality in the Rouxville District, Free State Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Rouxville District.
Referred material. None.
Remarks. Broom (1904) stated that the frontal was included in the orbital margin and considered the otic notch to have been closed posteriorly, as in the Late Triassic *Cyclotosaurus.* The specimen is likely to be mastodonsaurid but the exceedingly brief description and lack of figures renders any taxonomic assignment uncertain. The holotype could not be located in the SAM collections and is evidently lost.

Kestrosaurus dreyeri Haughton 1925
Holotype. SAM-PK-3452, a fragmentary skull, the fragments of which are set in plaster.
Locality and horizon. Farm Harmonia, Senekal District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.
Referred material. A mandibular fragment said to be associated with the holotype skull (Chernin 1978).
Remarks. Kestrosaurus dreyeri was initially described (Haughton 1925) as possessing, amongst other peculiarities, paired anterior palatal vacuities, circular nostrils and an interfrontal. The presence of these characters was apparently corroborated by Chernin (1978), who redescribed the holotype skull as well as a referred mandibular fragment. *K. dreyeri* has been variously considered an aberrant 'capitosaurid' (Welles & Cosgriff 1965; Chernin 1978), closely related to *Benthosuchus* (Romer 1947), or closely related to *Mastodonsaurus* (Shishkin 1980; Milner *et al.* 1990), primarily on the basis of the alleged presence of paired anterior palatal vacuities. More recent workers (Hancox *et al.* 1995; Shishkin *et al.* 1995) consider *K. dreyeri* a typical 'capitosaurid' closely related to *Parotosuchus.* However, Damiani (2001a) considered the holotype skull an indeterminate mastodonsaurid as it was based largely on a plaster reconstruction within which non-diagnostic mastodonsaurid fragments had been embedded.

Parotosuchus dirus Chernin 1978
Holotype. SAM-PK-434, fragments of a left and right lower jaw and associated cranial fragments.
Locality and horizon. An unknown locality near Aliwal North, Eastern Cape Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Aliwal North District.
Referred material. UMZC T167, a mastodonsaurid fragment from Aliwal North, Eastern Cape Province (Schoch & Milner 2000).
Remarks. The holotype pertains to a very large individual and is unusual in showing an additional row of teeth posterior to the usual post-symphyseal tooth row, and teeth on the anterior coronoid. The latter character is rare in stereospondyls but does occur in undescribed mandibles from the *Cynognathus* Assemblage Zone, probably referable to *Watsonisuchus* (RJD, pers. obs.). However, those mandibles are considerably smaller than that of *P. dirus,* differ significantly in the structure of the post-glenoid area, and usually lack any parasymphyseal teeth (RJD, pers. obs.). *Parotosuchus dirus* does not pertain

to *Parotosuchus* and probably represents a new genus, but additional material is required for a definitive diagnosis.

***Parotosaurus* sp.**

Material. UMZC T135, the posterior portion of a left mandible (Watson 1962).

Locality and horizon. Farm Winaarsbaken, Burgersdorp District (not 'Prince Albert District' of Schoch & Milner (2000)), Eastern Cape Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian.

Remarks. As the crucial post-glenoid area of the mandible is damaged the specimen is largely generically indeterminate. However, it likely pertains to *Wellesaurus africanus* which is known from this locality and is the most common mastodonsaurid in Subzone B of the *Cynognathus* biozone.

Rhinesuchidae Watson 1919

Rhinesuchus whaitsi Broom 1908

Rhinesuchus beaufortensis Boonstra 1940

Holotype. SAM-PK-1212, the basicranial region of a skull and associated cranial fragments.

Locality and horizon. Near Leeu-Gamka (formerly Fraserburg Road Station), Prince Albert District, Western Cape Province; *Tapinocephalus* Assemblage Zone, Late Permian.

Referred material. SAM-PK-3009, a near-complete skull and partial lower jaws (Haughton 1915b) from an unknown locality near Beaufort West, Western Cape Province. Skull fragments (unnumbered) from the farm Zeekoegat, Prince Albert District, Western Cape Province, mentioned by Broom (1908, 1912); *Tapinocephalus* Assemblage Zone, Late Permian. The posterior half of a skull from the farm Blaauw Krantz, Prince Albert District, Western Cape Province, mentioned by Haughton (1925); *Tapinocephalus* Assemblage Zone, Late Permian. SAM-PK-9135, the posterior end of a mandible (Watson 1962); farm Vogelfontein, Prince Albert District, *Tapinocephalus* Assemblage Zone, Late Permian. UMZC T64, a basicranial fragment (Watson 1962); farm Zeekoegat, Prince Albert District, Western Cape Province; *Tapinocephalus* Assemblage Zone, Late Permian.

Remarks. The Rhinesuchidae require a thorough morphological revision as inadequate data are available in the literature and most of the material is in need of preparation (RJD, pers. obs.). Consequently, the taxonomy and all accompanying remarks in this section are necessarily provisional pending a forthcoming revision by the authors. Haughton (1915b) briefly described a skull (SAM-PK-3009) which he referred to *R. whaitsi* but provided only photographs of the specimen and drawings of cross-sections through the left mandible. Watson (1919) figured the palate of *R. whaitsi* based on a sketch sent to him by Broom, and which Watson (1962) later considered to have probably been based on SAM-PK-3009. Haughton (1925) subsequently redescribed the holotype basicranial fragment and designated SAM-PK-3009 the 'paratype' for the species; however, this designation cannot hold as Broom (1908) did not designate a paratype. SAM-PK-3009 was later designated the holotype for the new species *Rhinesuchus beaufortensis* (Boonstra 1940), with which Watson (1962) agreed but which is here and in Schoch & Milner (2000) considered a junior synonym of *R. whaitsi.*

Uranocentrodon senekalensis van Hoepen 1917, Fig. 2F

Myriodon senekalensis van Hoepen 1911

Rhinesuchus major Broom 1912

Rhinesuchus senekalensis (van Hoepen) Haughton 1915b

Holotype. TM 75, the right side of a partial skull with attached lower jaw (van Hoepen 1911).

Locality and horizon. A sandstone quarry, the precise locality of which remains uncertain, near Senekal, Free State Province; *Dicynodon* Assemblage Zone, Late Permian.

Referred material. MA 60c1 and 60c1a, two partial skulls, described by Broom (1912) as *Rhinesuchus major,* and mentioned by van Hoepen (1911, 1915) as the specimens that had 'previously found their way to the Museum of the University College at Johannesburg'; three near-complete skeletons in numerous blocks of sandstone, all originally in the Transvaal Museum, Pretoria, and with which the holotype specimen, TM 75, is associated (van Hoepen 1915); NM QR1483, a near-complete skeleton in a sandstone block (Haughton 1915b); SAM-PK-2783, a partial left mandible with attached pieces of skull mentioned by Haughton (1915b); TM 185, a near-complete skull with attached lower jaw (Broom 1930). All known material of *Uranocentrodon senekalensis* is presumed to have come from the same unknown quarry near Senekal, a hypothesis supported by the similar lithology of the matrix associated with each specimen (Latimer *et al.* 2002).

Remarks. Uranocentrodon senekalensis was long considered from the Early Triassic *Lystrosaurus* Assemblage Zone (e.g. Kitching 1978) but has recently been shown (Latimer *et al.* 2002) to belong to the underlying *Dicynodon* Assemblage Zone, the assumption being that all of the known material was recovered from the same quarry near Senekal. In addition to the principal descriptions given by van Hoepen, Broom and Haughton, additional data on the species is provided by Watson (1962) and Findlay (1968).

Laccosaurus watsoni Haughton 1925, Fig. 2G

Lydekkerina kitchingi Broom 1950

Muchocephalus muchos Watson 1962

Uranocentrodon watsoni (Haughton) Ochev 1966

Muchocephalus kitchingi (Broom) Schoch & Milner 2000

Holotype. SAM-PK-4010, a near-complete skull.

Locality and horizon. Farm Ferndale, Graaff-Reinet District, Eastern Cape Province; *Dicynodon* (formerly *Daptocephalus*) Assemblage Zone, Late Permian (Kitching 1978).

Referred material. BP/1/215, the holotype (a near-complete skull) of *Lydekkerina kitchingi* Broom. BP/1/213, the holotype (a near-complete skull) of *Muchocephalus muchos* Watson. Both specimens were found in close association on the farm Ringsfontein, Murraysburg District (Kitching 1978); *Dicynodon* (formerly *Daptocephalus*) Assemblage Zone, Late Permian. An additional

92 specimens (reposited in the BPI, Johannesburg) from the same horizon on the adjoining farm Beeldhouersfontein were referred to *L. kitchingi* by Kitching (1977, 1978).

Remarks. It appears likely that the holotypes of *Lydekkerina kitchingi* (Broom 1950), which is based on a small skull, and *Muchocephalus muchos* (Watson 1962), a much larger skull, represent juvenile and adult individuals of the same species as they were recovered in close association from the same locality. As the holotype of *M. muchos* appears morphologically indistinguishable from that of *Laccosaurus watsoni* (Haughton 1925), both *L. kitchingi* and *M. muchos* are here considered subjective junior synonyms of *L. watsoni.* As far as can be determined the 92 additional specimens of *L. kitchingi* reported by Kitching (1977, 1978) consist exclusively of small, probably juvenile, skulls (RJD, pers. obs.). Kitching (1978) also mentions a paratype specimen of *L. kitchingi* from Ringsfontein; however, Broom (1950) did not designate a paratype.

Rhinesuchus capensis Haughton 1925

Rhinesuchus avenanti Boonstra 1940

Holotype. SAM-PK-7419, an incomplete skull.

Locality and horizon. Farm Spitzkop, Graaff-Reinet District, Eastern Cape Province; the horizon was given by Haughton (1925) as the '*Endothiodon* zone' (now corresponding to the *Tropidostoma* Assemblage Zone), and by Broom (1948) and Kitching (1978) as the '*Cistecephalus* zone', the latter now corresponding to both the *Tropidostoma* and *Cistecephalus* Assemblage zones (Rubidge 1995).

Referred material. SAM-PK-11489, the holotype (a skull) of *Rhinesuchus avenanti* Boonstra; farm Mynhardts Kraal, Beaufort West District, Western Cape Province. The horizon is stated as the '*Tapinocephalus* zone' by Boonstra (1940) and Kitching (1977), which now corresponds to both the *Tapinocephalus* and *Pristerognathus* Assemblage zones.

Remarks. The holotype of *R. capensis* is the largest known rhinesuchid skull with a high degree of ossification of the cranial bones (Haughton 1925). Consequently, sutures are poorly shown. Note that figures of *R. capensis* given by Haughton (1925) are inaccurate in that the skull is depicted as too short and broad, whereas it should be somewhat more slender and elongated (RJD, pers. obs.). The holotype of *R. avenanti* is considerably smaller but is otherwise very similar morphologically to *R. capensis,* and is here considered a junior synonym of the latter. In contrast, Watson (1962) and Schoch & Milner (2000) considered *R. avenanti* a junior synonym of *Rhinesuchoides tenuiceps* (Olson & Broom 1937), probably on the basis of having a similarly slender skull.

Broomistega putterilli (Broom) Shishkin & Rubidge 2000, Fig. 2H

Lydekkerina putterilli Broom 1930

Holotype. TM 184, the posterior half of a skull and an associated mandibular fragment.

Locality and horizon. Harrismith Commonage, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. BP/1/5058, a complete skull with lower jaw in articulation, and associated dermal pectoral girdle (Shishkin & Rubidge 2000); Ndanyane Hill, farm Hartebeest Spruit, Bergville District, KwaZulu-Natal. BP/1/3241, a partially disarticulated skeleton including skull and lower jaw (Shishkin & Rubidge 2000); farm Admiralty Estates, near Oliviershoek Pass, Bergville District, KwaZulu-Natal. Both specimens from the *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. Described originally by Broom (1930) as a lydekkerinid closely related to *Lydekkerina huxleyi,* but shown by Shishkin & Rubidge (2000) to be a rhinesuchid and the only one known from the Triassic.

Rhinesuchoides tenuiceps Olson & Broom 1937, Fig. 2I

Rhinesuchus rubidgei Broom 1948

Holotype. FMNH UC 1519, a skull and partial left lower jaw.

Locality and horizon. Stated by Olson & Broom (1937) as '*Tapinocephalus* zone, 2 miles east of Stinkfontein'; this is probably the farm Stinkfontein located in the Prince Albert District, Western Cape Province, in which the *Tapinocephalus* Assemblage Zone is exposed (Kitching 1977).

Referred material. RC 73, the holotype (a skull) of *Rhinesuchus rubidgei* Broom (Schoch & Milner 2000); Farm Wimbledon (Welgevonden), Graaff-Reinet District, Eastern Cape Province; *Cistecephalus* Assemblage Zone, Late Permian.

Remarks. The synonomy of *Rhinesuchus rubidgei* and *Rhinesuchoides tenuiceps* was also accepted by Schoch & Milner (2000), both specimens being based on similarly sized skulls with near-identical proportions. Schoch & Milner (2000) also referred to *R. tenuiceps* three specimens, BP/1/2741, BP/1/2931 and BP/1/2958, which they state as pertaining to the *Tapinocephalus* Assemblage Zone. However, the latter two specimens are small rhinesuchid skulls associated with those collected by Kitching on the farm Beeldhouersfontein in the Murraysburg District (Kitching (1977, 1978), which were considered to belong to '*Lydekkerina' kitchingi* (see *Laccosaurus watsoni*) and are from the *Dicynodon* Assemblage Zone. BP/1/2741 is a partial pelvis of the therapsid *Lystrosaurus* from the *Lystrosaurus* Assemblage Zone; the number as stated is probably a typographical error.

Rhinesuchidae indet.

Eryops oweni Lydekker 1890a, *nomen dubium*

Eryops africanus Lydekker 1890b

Rhinesuchus africanus (Lydekker) Broom 1908

Holotype. BMNH R466, an incomplete right mandibular ramus.

Locality and horizon. An unknown locality in the Karoo.

Referred material. BMNH R470, an intercentrum (Lydekker 1890a); locality and horizon unknown but apparently associated with the holotype. SAM-PK-3010, a fragmentary skull and lower jaw (Haughton 1915b); farm Dunedin, Beaufort West District, Western Cape Province; the horizon was stated by Haughton (1915b) as '*Cistecephalus* zone', although Kitching (1977) stated that the

locality pertains to the former '*Endothiodon* zone', which now corresponds to the *Tropidostoma* Assemblage Zone (Rubidge 1995).

Remarks. The holotype specimen almost certainly pertains to a rhinesuchid because of the dense shagreen field covering the coronoid series and the slightly antero-posteriorly compressed marginal teeth. Haughton's (1915b) referred specimen includes a fragmentary and badly damaged skull and mandible; however, there is no reason to consider this specimen conspecific with Lydekker's holotype and the state of preservation of SAM-PK-3010 precludes any taxonomic referral.

Rhinesuchus broomianus von Huene 1931, *nomen dubium*

Holotype. GPIT Huene 1931 F.1, a partial skull.

Locality and horizon. Farm Kuilspoort, Beaufort West District, Western Cape Province; *Tropidostoma* (previously *Endothiodon*) Assemblage Zone, Late Permian.

Referred material. None.

Remarks. This species was considered valid by Schoch & Milner (2000) whose diagnosis was based principally on the skull being somewhat broader than in other rhinesuchids. However, the skull of *R. broomianus* has evidently undergone considerable dorso-ventral compaction and is poorly preserved, rendering any comparisons with other rhinesuchids difficult.

Rhytidosteidae Huene 1920

Rhytidosteus capensis Owen 1884

Holotype. BMNH R455, the antorbital portion of a skull with the anterior parts of the lower jaw in articulation, and the posterior part of the right mandible.

Locality and horizon. Given by Owen as 'Beersheba', Free State Province; Horizon unknown because of ambiguous locality details. Considered variably as from either the *Lystrosaurus* (Kitching 1978; Cosgriff & Zawiskie 1979; Shishkin 1994) or *Cynognathus* (Huene 1920; Romer 1947; Warren & Black 1985) Assemblage Zones.

Referred material. BMNH R503, an interotic fragment, a basicranial fragment, and a clavicular fragment (Lydekker 1890b), all considered by Lydekker to have been associated with the holotype; locality and horizon as for the holotype.

Remarks. Additional descriptions of *Rhytidosteus capensis* have been provided by Watson (1919), Huene (1920), Romer (1947) and Cosgriff (1965). Romer (1947) considered *R. capensis* conspecific with the trematosaurid *Microposaurus casei* (Haughton 1925), reconstructing the former using the outline of the latter and transferring *R. capensis* to the Trematosauridae. Cosgriff (1965) considered the association of *R. capensis* with *M. casei* to have been erroneous and returned the former to the Rhytidosteidae. Warren & Black (1985) suggested that *R. capensis* may be a composite of rhytidosteid and trematosaurid fragments, and left the species *incertae sedis* within the Trematosauroidea (*sensu* Warren & Black 1985: Rhytidosteidae + Trematosauridae). However, most workers (Cosgriff 1984; Milner 1990; Shishkin 1994; Schoch & Milner 2000) consider *R. capensis* a valid rhytidosteid. Schoch & Milner (2000) listed the fragmentary Russian species *Rhytidosteus uralensis* (Shishkin 1994) as a junior synonym of *R. capensis.* Although this assumption is reasonable, we prefer to leave *R. uralensis* as a separate species pending more complete material.

Pneumatostega potamia Cosgriff & Zawiskie 1979, Fig. 3A

Holotype. BP/1/981, a sandstone fragment containing the impression of a partial skull roof.

Locality and horizon. Farm Tafelberg, Middelburg District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. SAM-PK-11188, associated fragments of a skull, lower jaw, dermal shoulder girdle and vertebral column (Cosgriff & Zawiskie 1979); farm Goede Hoop, Colesberg District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Trematosauridae Watson 1919

Trematosuchus sobeyi (Haughton) Watson 1919, Fig. 3B

Trematosaurus sobeyi Haughton 1915a

Aphaneramma sp. Hammer 1987, in part.

Holotype. SAM-PK-2779, a complete skull.

Locality and horizon. Sobey's Quarry, Queenstown, Eastern Cape Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Referred material. SAM-PK-5136, the middle portion of a skull (Haughton 1925); locality and horizon as for the holotype. NM QR3263A and B, the anterior part of a snout and a palatal fragment, respectively (Shishkin & Welman 1994); farm Verdun, Paul Roux District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Remarks. The referred specimen, SAM-PK-5136, was considered an indeterminate long-snouted (i.e. lonchorhynchine) trematosaurid and thus transferred to *Aphaneramma* sp. by Hammer (1987). However, SAM-PK-5136 comes from the same locality as the holotype of *Trematosuchus sobeyi* and is therefore reasonably considered referable to that taxon. The difficulty in placing SAM-PK-5136 taxonomically stems from the morphological similarity in postorbital skull morphology between short and long-snouted trematosaurids. A redescription of SAM-PK-5136 and all other supposed lonchorhynchines from the Karoo is in progress by the senior author.

Microposaurus casei Haughton 1925, Fig. 3C

Rhytidosteus casei Shishkin 1964

Holotype. SAM-PK-6556, a complete skull.

Locality and horizon. Exposures just above the Wonderboom Bridge, Burgersdorp District, Eastern Cape Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian.

Referred material. None.

Remarks. Considered by Romer (1947) and Shishkin (1964) to be congeneric with the fragmentary rhytidosteid *Rhytidosteus capensis,* but shown by Cosgriff (1965) to be a trematosaurid. The species was later excluded from the Trematosauridae by Hammer (1987), but included by

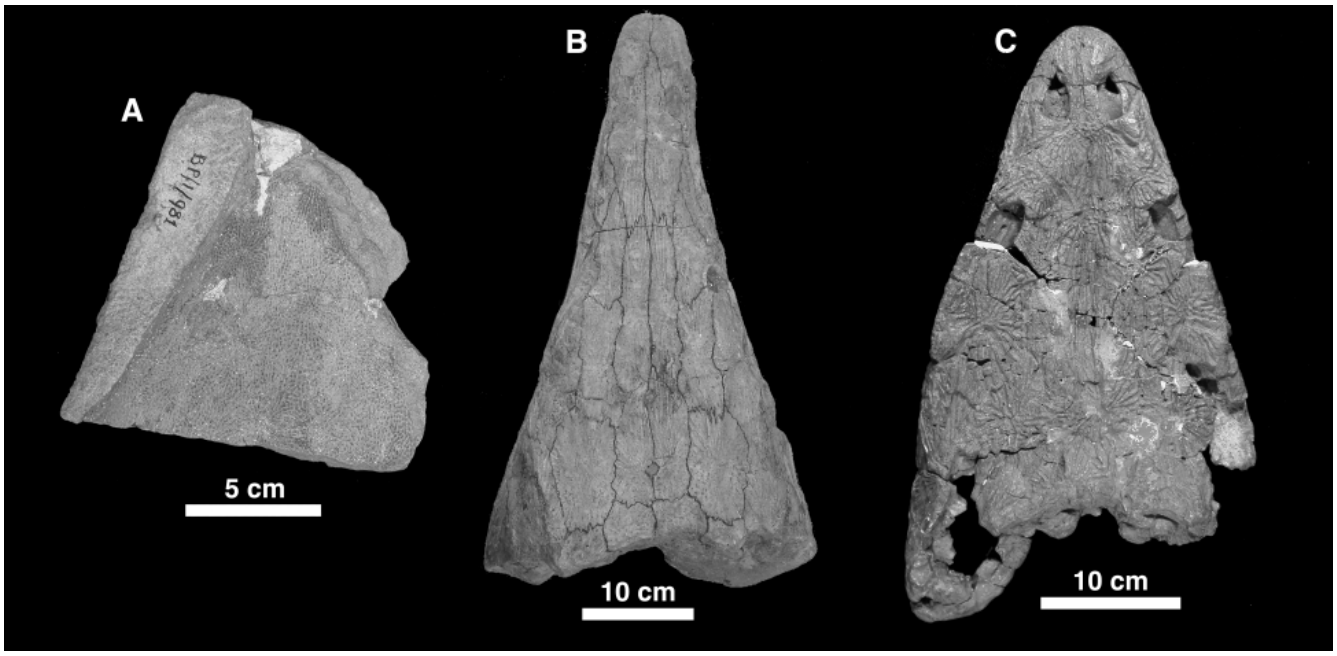


Figure 3. Photographs (in dorsal view) of the skulls of South African temnospondyls. **A**, *Pneumatostega potamia,* holotype, BP/1/981; **B**, *Trematosuchus sobeyi,* holotype, SAM-PK-2779; **C**, *Microposaurus casei,* holotype, SAM-PK-6556.

Warren & Black (1985), Hellrung (1987) and Schoch & Milner (2000). The latter authors suggested close affinities with *Tertrema* from the Early Triassic of Spitzbergen. However, the morphology of *M. casei,* currently being redescribed following additional preparation by the senior author, points strongly to affinities with the Russian 'platystegid' *Inflectosaurus amplus* (Shishkin 1960).

Trematosauridae indet.

Trematosaurus kannemeyeri Broom 1909, *nomen dubium*
Aphaneramma kannemeyeri (Broom) Huene 1920
Trematosuchus kannemeyeri (Broom) Zittel 1923
Gonioglyptus kannemeyeri (Broom) Huene 1925
Aphaneramma sp. Hammer 1987, in part

Holotype. SAM-PK-1329, a portion of the middle part of a badly weathered skull, including the orbits.

Locality and horizon. An unknown locality in the Free State Province, then known as the 'Orange River Colony' (Broom 1909); horizon unknown, but suggested as 'Upper Beaufort Beds' (equivalent to the *Cynognathus* Assemblage Zone) by Haughton (1925), and adopted by all subsequent workers.

Referred material. None.

Remarks. Widely considered an indeterminate, *Aphaneramma*-like lonchorhynchine by recent workers (Hammer 1987; Welles 1993; Shishkin & Welman 1994), and listed as a valid lonchorhynchine, *Aphaneramma kannemeyeri,* by Schoch & Milner (2000). In contrast, Damiani *et al.* (2000) considered *Trematosaurus kannemeyeri* referrable to either a long or short-snouted trematosaurid, and declared the specimen a *nomen dubium.* Subsequent re-examination by the senior author has confirmed its lonchorhynchine affinities; however, its poor state of preservation precludes any further taxonomic placement and the species should remain a *nomen dubium.* A redescription is currently in progress by the senior author.

A recently discovered lonchorhynchine from the *Lystrosaurus* Assemblage Zone was reported by Damiani & Welman (2001) as representing an undoubted lonchorhynchine from that biozone. This specimen, NM QR3424, is represented by a partial snout and may belong to the same species as '*Trematosaurus' kannemeyeri.* A full description will be the subject of a forthcoming publication.

Trematosauridae gen. et. sp. indet.

Material. CGP 1/5, a complete but damaged right mandibular ramus (Damiani *et al.* 2000).

Locality and horizon. Farm Perdelaagte (an annexe of the farm Heuningkrans 26), Burgersdorp District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. This specimen appears to belong to a short-snouted trematosaurid such as *Trematosaurus* or *Trematosuchus,* and, along with NM QR3424, represents the second trematosaurid taxon from the *Lystrosaurus* Assemblage Zone. The specimen is of further importance as it comes from high in the *Lystrosaurus* Assemblage Zone, in strata which have been postulated to pertain to an 'intermediate' biozone between the *Lystrosaurus* and *Cynognathus* biozones (Neveling *et al.* 1999).

Stereospondyli indet.

Laccocephalus insperatus Watson 1919, *nomen dubium*

Holotype. BMNH R532, an incomplete skull in a sandstone nodule.

Locality and horizon. Stated by Watson (1919) as 'near Mr Hope's farm, Orange Free State'; horizon unknown.

Referred material. None.

Remarks. The poor preservation of *L. insperatus* renders any taxonomic assignment uncertain. However, in size and general outline the specimen is almost certainly a

stereospondyl. In particular, the presence of a *crista muscularis* of the parasphenoid and a median, raised area on the cultriform process, as alluded to by Watson (1919), suggest that *L. insperatus* may be a rhinesuchid or mastodonsaurid. However, there is neither sufficient morphological nor stratigraphic data to suggest that *L. insperatus* is synonymous with *Uranocentrodon senekalensis* (contra Schoch & Milner 2000).

Stereospondyli gen. et. sp. indet.

Material. BP/1/4935, a fragment of a mandibular ramus from the farm Mequatling, Clocolan District, Free State Province (Warren & Damiani 1999); Lower Elliot Formation, Late Triassic.

Remarks. Likely to pertain to a chigutisaurid, as with all of the other known temnospondyl material from the Elliot Formation (see Chigutisauridae).

Temnospondyli indet.

Petrophryne major Owen 1876b, *nomen dubium*

Bothriceps major (Owen) Lydekker 1890b

Holotype. BMNH R4145, a sandstone block containing a poorly preserved partial skull, largely as impression. Originally held in the museum of the Geological Society of London under the catalogue number S.A.119.

Locality and horizon. Collection data associated with the holotype states the horizon and locality as the 'Stormberg Beds', 'Southern margin of the Stormberg Range'.

Ptychosphenodon browni Seeley 1907, *nomen dubium*

Holotype. BMNH R3503, a mandibular fragment.

Locality and horizon. An unknown locality near Aliwal North, Eastern Cape Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Aliwal North District.

Syphonodon thecomastodon Seeley 1908, *nomen dubium*

Holotype. BMNH R3609, a large temnospondyl tooth.

Locality and horizon. Farm Wonderboom, Burgersdorp District, Eastern Cape Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Burgersdorp District.

Phrynosuchus whaitsi Broom 1913, *nomen dubium*

Rhinesuchus sp. Chernin & Kitching 1977

Holotype. SAM-PK-2357, a crushed, poorly preserved skull and articulated partial postcranial skeleton in a sandstone nodule.

Locality and horizon. Farm Droogvoets Fontein, Fraserburg District, Western Cape Province; Horizon uncertain, but suggested by Broom (1913) as 'upper part of the *Endothiodon* Zone', and more recently (Chernin & Kitching 1977) as either uppermost *Tapinocephalus* Zone or lowermost *Cistecephalus* Zone. These horizons now correspond, respectively, to the *Pristerognathus* and *Tropidostoma* Assemblage Zones, of Late Permian age.

Remarks. Broom (1913) made no attempt to place the specimen taxonomically, but it was later considered an indeterminate rhinesuchid by Chernin & Kitching (1977). Schoch & Milner (2000) followed this assignation. However, re-examination of the specimen by the senior author failed to reveal any resemblance to rhinesuchids or any characters which could place the specimen taxonomically.

CONCLUSIONS

The Karoo of South Africa boasts a rich and varied temnospondyl fauna that is amongst the most diverse in the world, with 10 higher-level taxa recorded to date. This record is dominated by predominantly large temnospondyls of the clade Stereospondyli.

The Palaeozoic temnospondyl record in the Karoo is at present restricted to one higher-level taxon, the Rhinesuchidae, despite the fact that six of the eight biozones of the Beaufort Group are of Permian age. It is unclear, however, whether this reflects a true paucity (or absence) of other higher-level taxa or a preservational bias (Kitching 1978). Members of the Rhinesuchidae appear to be endemic to Gondwana, and have been recorded elsewhere from the Upper Permian of what is now Malawi (Watson 1962), India (Werneburg & Schneider 1996) and Brazil (Barberena 1998; Barberena & Dias 1998). However, the diversity of rhinesuchids is greater in the Karoo than anywhere else in Gondwana, and only in the Karoo are rhinesuchids known to have survived the end-Permian extinction event. These facts are significant because the Rhinesuchidae are widely regarded as the most basal stereospondyls (Milner 1990; Schoch & Milner 2000; Yates & Warren 2000).

The Mesozoic sequence plays host to all 10 higher-level temnospondyl taxa known from the Karoo, distributed as follows. The *Lystrosaurus* Assemblage Zone contains seven higher-level taxa, the Amphibamidae, Tupilakosauridae, Rhinesuchidae, Lydekkerinidae, Rhytidosteidae, Mastodonsauridae and Trematosauridae. The overlying *Cynognathus* Assemblage Zone hosts the last two of these taxa in addition to the Brachyopidae, Laidleriidae, and, possibly, the Rhytidosteidae. The now greater diversity of higher-level temnospondyl taxa in the *Lystrosaurus* biozone is noteworthy because of the previously held notion that the *Cynognathus* biozone contained a greater diversity of temnospondyls. This shift in diversity has occurred only recently, however, with the resurgence in studies of Beaufort Group temnospondyls. The remaining higher-level taxon, the Chigutisauridae, is at present known only from the Late Triassic–Early Jurassic Elliot Formation.

Finally, it is particularly noteworthy that the *Lystrosaurus* Assemblage Zone plays host to a relict member of the dvinosaurian radiation (*Thabanchuia*), the last surviving member of the Dissorophoidea (*Micropholis*), and the only Triassic rhinesuchid (*Broomistega*). These facts, combined with the high diversity of rhinesuchids in the Permian of the Karoo, lend strong support to the hypothesis that the initial radiation of the Stereospondyli occurred in a 'safe haven' that was located in Gondwana (Yates & Warren 2000; Warren *et al.* 2000). The evidence for a Gondwanan origin and radiation also suggests that the exact position of the 'safe haven' may have been southern Africa. However, it remains unclear whether the great stereospondyl

radiation began in the Late Permian (Yates & Warren 2000) or in the earliest Triassic (Milner 1990).

We are grateful to Mrs Elizabeth Latimer-Schaafsma (BPI Palaeontology) for generously sharing information on rhinesuchids, Dr Alain Renaut (BPI Palaeontology) for locality information, and Dr Andrew Milner (Birkbeck College, London) for information on *Micropholis stowii* and '*Petrophryne major*'. The senior author would also like to thank Dr Roger Smith of the South African Museum, Cape Town, for access to their temnospondyl collections, and the University of the Witwatersrand and National Research Foundation of South Africa for financial support. Drs Andrew Milner and Adam Yates refereed the manuscript and offered helpful suggestions for its improvement.

REFERENCES

ANDERSON, J.M. & ANDERSON, H.M. 1984. The fossil content of the Upper Triassic Molteno Formation, South Africa. *Palaeontologia africana* **25**, 39–59.

ANDERSON, J.M. & CRUICKSHANK, A.R.I. 1978. The biostratigraphy of the Permian and the Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontologia africana* **21**, 15–44.

ANDERSON, J.M., ANDERSON, H.M. & CRUICKSHANK, A.R.I. 1998. Late Triassic ecosystems of the Molteno/Lower Elliot biome of southern Africa. *Palaeontology* **41**, 387–421.

BARBERENA, M.C. 1998. *Australerpeton cosgriffi* n.g., n.sp., a Late Permian rhinesuchoid amphibian from Brazil. *Anais da Academia Brasileira de Ciências* **70**, 125–137.

BARBERENA, M.C. & DIAS, E.V. 1998. On the presence of a short-snouted rhinesuchoid amphibian in the Rio do Rasto Formation (Late Permian of Paraná Basin, Brazil). *Anais da Academia Brasileira de Ciências* **70**, 465–468.

BOLT, J.R. 1991. Lissamphibian origins. **In**: Schultze, H.P. & Trueb, L., (eds), *Origins of the Higher Groups of Tetrapods – Controversy and Consensus,* 194–222. Ithaca, Cornell University Press.

BOONSTRA, L.D. 1940. Twee nuwe ragitome Labirintodontiërs. *Oorgedruk uit Tydskrif vir Wetenskap en Kuns* **1**,195–198.

BOULENGER, G.A. 1902. Amphibia. **In:** Encyclopaedia Britannica (10th edn), 381–384.

BOY, J.A. 1985. Über *Micropholis,* den letzten Überlebenden der Dissorophoidea (Amphibia, Temnospondyli; Unter-Trias). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1985**, 29–45.

BROILI, F. & SCHRÖDER, J. 1937a. Beobachtungen an Wirbeltieren der Karrooformation. XXV. Über *Micropholis* Huxley. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften München* **1937**, 19–38.

BROILI, F. & SCHRÖDER, J. 1937b. Beobachtungen an Wirbeltieren der Karrooformation. XXV. Über *Lydekkerina* Broom. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften München* **1937**, 39–57.

BROILI, F. & SCHRÖDER, J. 1937c. Beobachtungen an Wirbeltieren der Karrooformation. XXVII. Über einen Capitosauriden aus der *Cynognathus*-Zone. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften München* **1937**, 98–117.

BROOM, R. 1903. On a new stegocephalian (*Batrachosuchus browni*) from the Karroo beds of Aliwal North, South Africa. *Geological Magazine* (Decade IV) **10**, 499–501.

BROOM, R. 1904. On a new South African labyrinthodont (*Cyclotosaurus albertyni*). *Records of the Albany Museum* **1**,178–180.

BROOM, R. 1908. On a new labyrinthodont *Rhinesuchus whaitsi,* from the Permian beds of South Africa. *Annals of the South African Museum* **4**, 373–376.

BROOM, R. 1909. Notice of some new South African fossil amphibians and reptiles. *Annals of the South African Museum* **7**, 270–278.

BROOM, R. 1912. Note on the temnospondylous stegocephalian, *Rhinesuchus. Transactions of the Geological Society of South Africa* **14**, 79–81.

BROOM, R. 1913. On a new South African stegocephalian (*Phrynosuchus whaitsi*). *Annals of the South African Museum* **12**, 6–7.

BROOM, R. 1915. On the Triassic stegocephalians *Brachyops, Bothriceps,* and *Lydekkerina* gen. nov. *Proceedings of the Zoological Society of London* **1915**, 363–368.

BROOM, R. 1930. Notes on some labyrinthodonts in the Transvaal Museum. *Annals of the Transvaal Museum* **14**, 1–10.

BROOM, R. 1948. A contribution to our knowledge of the vertebrates of the Karroo Beds of South Africa. *Transactions of the Royal Society of Edinburgh* **61**, 577–629.

BROOM, R. 1950. A new small labyrinthodont from the Karroo beds of South Africa. *Annals of the Transvaal Museum* **21**, 251–252.

CAIRNCROSS, B., ANDERSON, J.M. & ANDERSON, H.M. 1995. Palaeoecology of the Triassic Molteno Formation, Karoo Basin, South Africa sedimentological and palaeontological evidence. *South African Journal of Geology* **98**, 452– 478.

CARROLL, R.L. & WINER, L. 1977. Patterns of amphibian evolution: an extended example of the incompleteness of the fossil record. Appendix 13. Classification of amphibians and list of genera and species known as fossils. **In:** Hallam, A. (ed.), *Patterns of Evolution,* 405–437. Amsterdam, Elsevier.

CATUNEANU, O., HANCOX, P.J. & RUBIDGE, B.S. 1998. Reciprocal flexural behaviour and contrasting stratigraphies: a new basin development model for the Karoo retroarc foreland system, South Africa. *Basin Research* **10**, 417–439.

CHERNIN, S. 1977. A new brachyopid, *Batrachosuchus concordi* sp. nov. from the Upper Luangwa Valley, Zambia with a redescription of *Batrachosuchus browni* Broom, 1903. *Palaeontologia africana* **20**, 87–109.

CHERNIN, S. 1978. Three capitosaurs from the Triassic of South Africa: *Parotosuchus africanus* (Broom 1909); *Kestrosaurus dreyeri* Haughton 1925, and *Parotosuchus dirus* sp. nov. *Palaeontologia africana* **21**, 79–100.

CHERNIN, S. & KITCHING, J.W. 1977. A reassessment of *Phrynosuchus whaitsi* Broom. *Palaeontologia africana* **20**, 111–113.

COLBERT, E.H. & COSGRIFF, J.W. 1974. Labyrinthodont amphibians from Antarctica. *American Museum Novitates* **2552**, 1–30.

COSGRIFF, J.W. 1965. A new genus of Temnospondyli from the Triassic of Western Australia. *Journal of the Royal Society of Western Australia* **48**, 65–90.

COSGRIFF, J.W. 1984. The temnospondyl labyrinthodonts of the earliest Triassic. *Journal of Vertebrate Paleontology* **4**, 30–46.

COSGRIFF, J.W. & ZAWISKIE, J.M. 1979. A new species of the Rhytidosteidae from the *Lystrosaurus* Zone and a review of the Rhytidosteoidea. *Palaeontologia africana* **22**, 1–27.

DALY, E. 1994. The Amphibamidae (Amphibia: Temnospondyli), with a description of a new genus from the Upper Pensylvanian of Kansas. *The University of Kansas Museum of Natural History Miscellaneous Publications* **85**, 1–59.

DAMIANI, R.J. 1999. *Parotosuchus* (Amphibia, Temnospondyli) in Gondwana: biostratigraphic and palaeobiogeographic implications. *South African Journal of Science* **95**, 458–460.

DAMIANI, R.J. 2001a. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). *Zoological Journal of the Linnean Society* **133**, 379–482.

DAMIANI, R.J. 2001b. *Parotosuchus* (Amphibia, Temnospondyli) from the *Cynognathus* Assemblage Zone (Early Triassic) of South Africa: cranial morphology and relationships. *Alcheringa* **25**, 351–379.

DAMIANI, R.J. 2004. Temnospondyls from the Beaufort Group (Karoo Basin) of South Africa and their biostratigraphy. *Gondwana Research* **7**: 165–173.

DAMIANI, R.J. & HANCOX, P.J. 2003. New mastodonsaurid temnospondyls from the *Cynognathus* Assemblage Zone (Upper Beaufort Group; Karoo Basin) of South Africa. *Journal of Vertebrate Paleontology* **23**, 55–67.

DAMIANI, R.J. & JEANNOT, A.M. 2002. A brachyopid temnospondyl from the lower *Cynognathus* Assemblage Zone in the northern Karoo Basin, South Africa. *Palaeontologia africana* **38**, 57–69.

DAMIANI, R.J. & KITCHING, J.W. 2003. A new brachyopid temnospondyl from the *Cynognathus* Assemblage Zone, Upper Beaufort Group, South Africa. *Journal of Vertebrate Paleontology* **23**, 68–79.

DAMIANI, R.J., NEVELING, J. & HANCOX, P.J. 2001. First record of a mastodonsaurid (Temnospondyli, Stereospondyli) from the Early Triassic *Lystrosaurus* Assemblage Zone (Karoo Basin) of South Africa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **221**, 133–144.

DAMIANI, R.J., NEVELING, J. & HANCOX, P.J. & RUBIDGE, B. 2000. First trematosaurid temnospondyl from the *Lystrosaurus* Assemblage Zone of South Africa and its biostratigraphic implications. *Geological Magazine* **137**, 659–665.

DAMIANI, R.J. & WELMAN, J. 2001. A long-snouted trematosaurid amphibian from the Early Triassic of South Africa. *South African Journal of Science* **97**, 318–320.

FINDLAY, G.H. 1968. On the structure of the skin in *Uranocentrodon* (*Rhinesuchus*) *senekalensis* Van Hoepen. *Palaeontologia africana* **11**, 15–22.

GOW, C.E. 1977. On a supposed skin impression of *Procolophon. Palaeontologia africana* **20**, 119.

HAMMER, W.R. 1987. Paleoecology and phylogeny of the Trematosauridae. *Geophysical Monograph* **41**, 73–83.

HANCOX, P.J. 1998. *A stratigraphic, sedimentological and palaeoenvironmental synthesis of the Beaufort-Molteno contact in the Karoo Basin.* Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

HANCOX, P.J. 2000. The continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie Teil I* **1998**, 1285–1324.

HANCOX, P.J., DAMIANI, R.J. & RUBIDGE, B.S. 2000. First occurrence of

Paracyclotosaurus (Temnospondyli, Capitosauridae) in the Karoo Basin of South Africa and its biostratigraphic implications. *South African Journal of Science* **96**, 135–137.
HANCOX, P.J. & RUBIDGE, B.S. 1997. The role of fossils in interpreting the development of the Karoo Basin. *Palaeontologia africana* **33**, 41–54.
HANCOX, P.J., SHISHKIN, M.A., RUBIDGE, B.S. & KITCHING, J.W. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical implications. *South African Journal of Science* **91**, 143–144.
HAUGHTON, S.H. 1915a. Investigations in South African fossil reptiles and Amphibia (Parts 1 to 4). *Annals of the South African Museum* **12**, 47–63.
HAUGHTON, S.H. 1915b. Investigations in South African fossil reptiles and Amphibia (Parts 5–9). *Annals of the South African Museum* **12**, 65–106.
HAUGHTON, S.H. 1925. Investigations in South African fossil reptiles and Amphibia (Part 13). *Annals of the South African Museum* **22**, 227–261.
HELLRUNG, H. 1987. Revision von *Hyperokynodon keuperinus* Plieninger (Amphibia: Temnospondyli) aus dem Schilfsandstein von Heilbronn (Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* **136**, 1–28.
HOPSON, J.A. 1984. Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. *Palaeontologia africana* **25**, 181–201.
HUENE, F. von 1920. *Gonioglyptus,* ein alttriassischer Stegocephale aus Indien. *Acta Zoologica* **1**, 433–464.
HUENE, F. von 1925. Die südafrikanische Karroo-Formation als geologisches und faunistisches Lebensbild. *Fortschritte der Geologie und Palaeontologie* **12**, 1–124.
HUENE, F. von 1931. Beitrag zur Kenntnis der Fauna der südafrikanischen Karrooformation. *Geologische und Palaeontologische Abhandlungen (N.S)* **18**, 157–228.
HUENE, F. von 1956. *Paläontologie und phylogeny der niederen Tetrapoden.* VEB Gustav Fischer Verlag, Jena.
HUXLEY, T.H. 1859. On some amphibian and reptilian remains from South Africa and Australia. *Quarterly Journal of the Geological Society* **15**, 642–658.
IVAKHNENKO, M.F., GOLUBEV, V.K., GUBIN, Y.M., KALANDADZE, N.N., NOVIKOV, I.V., SENNIKOV, A.G. & RAUTIAN, A.S. 1997. *Permian and Triassic tetrapods of Eastern Europe.* Moscow, GEOS (in Russian).
JOHNSON, M.R., VAN VUUREN, C.J., VISSER, J.N.J., COLE, D.I., DeVILLE WICKENS, H., CHRISTIE, A.D.M. & ROBERTS, D.L. 1997. The foreland Karoo Basin, South Africa. **In**: Selley, R.C. (ed), *African Basins. Sedimentary Basins of the World,* 269–317. Amsterdam, Elsevier.
KEYSER, A.W. & SMITH, R.M.H. 1979. Vertebrate biozonation of the Beaufort Group with special reference to the western Karoo Basin. *Annals of the Geological Survey of South Africa* **12**, 1–35.
KITCHING, J.W. 1957. A new small stereospondylous labyrinthodont from the Triassic beds of South Africa. *Palaeontologia africana* **5**, 67–82.
KITCHING, J.W. 1963. Notes on some fossil pockets and bone beds in the *Cynognathus*-Zone in the Burghersdorp and Lady Frere districts. *Palaeontologia africana* **8**, 113–118.
KITCHING, J.W. 1977. The distribution of the Karroo vertebrate fauna. *Bernard Price Institute for Palaeontological Research, Memoir* **1**, 1–131.
KITCHING, J.W. 1978. The stratigraphic distribution and occurrence of South African fossil Amphibia in the Beaufort Beds. *Palaeontologia africana* **21**, 101–112.
KITCHING, J.W. & RAATH, M.A. 1984. Fossils from the Elliot and Clarens formations (Karoo Sequence) of the northeastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. *Palaeontologia africana* **25**, 111–125.
KUHN, O. 1933. Labyrinthodontia. *Fossilium Catalogus. I: Animalia* **61**, 1–114.
KUHN, O. 1960. Die Familien der fossilen Amphibien und Reptilien. *Naturforschende Gesellschaft Bamberg* **37**, 20–52.
LATIMER, E.M., HANCOX, P.J., RUBIDGE, B.S., SHISHKIN, M.A. & KITCHING, J.W. 2002. The temnospondyl amphibian *Uranocentrodon,* another victim of the end-Permian extinction event. *South African Journal of Science* **98**, 191–193.
LUCAS, S.G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**, 347–384.
LYDEKKER, R. 1885. The Reptilia and Amphibia of the Maleri and Denwa groups. *Palaeontologia Indica (Ser. IV. Indian pre-Tertiary Vertebrata)* **1(5)**, 30–38.
LYDEKKER, R. 1889. Note on the occurrence of a species of *Bothriceps* in the Karoo system of South Africa. *Annals and Magazine of Natural History* **6**, 475–476.
LYDEKKER, R. 1890a. On two new species of labyrinthodonts. *Quarterly Journal of the Geological Society* **46**, 289–294.
LYDEKKER, R. 1890b. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part IV.* London, Taylor and Francis.
MARYANSKA, T. & SHISHKIN, M.A. 1996. New cyclotosaurid (Amphibia: Temnospondyli) from the Middle Triassic of Poland and some problems of interrelationships of capitosauroids. *Prace Muzeum Ziemi* **43**, 53–83.
MILNER, A.R. 1990. The radiations of temnospondyl amphibians. *Systematics Association Special Volume* **42**, 321–349.
MILNER, A.R., GARDINER, B.G., FRASER, N.C. & TAYLOR, M.A. 1990. Vertebrates from the Middle Triassic Otter Sandstone Formation of Devon. *Palaeontology* **33**, 873–892.
MODESTO, S.P. 1996. *Noteosaurus africanus* Broom is a nomen dubium. *Journal of Vertebrate Paleontology* **16**, 172–174.
MOODIE, R.L. 1910. The Amphibia of the Mazon Creek Shales. *Science* (n.s.) **31**, 233–234.
MORALES, M. & SHISHKIN, M.A. 2002. A re-assessment of *Parotosuchus africanus* (Broom), a capitosauroid temnospondyl amphibian from the Triassic of South Africa. *Journal of Vertebrate Paleontology* **22**, 1–11.
NEVELING, J., RUBIDGE, B.S. & HANCOX, P.J. 1999. A lower *Cynognathus* Assemblage Zone fossil from the Katberg Formation (Beaufort Group, South Africa). *South African Journal of Science* **95**, 555–556.
NIELSEN, E. 1954. *Tupilakosaurus heilmani* Nielson n. g. et. n. sp., an interesting batrachomorph from the Triassic of East Greenland. *Meddelelser om Grønland* **72**, 1–33.
OCHEV, V.G. 1966. *Systematics and phylogeny of capitosauroid labyrinthodonts.* Saratov, Saratov State University Press (in Russian).
OCHEV, V.G. & SHISHKIN, M.A. 1989. On the principles of global correlation of the continental Triassic on the tetrapods. *Acta Palaeontologica Polonica* **34**, 149–173.
OELOFSEN, B.W. 1981. *An anatomical and systematic study of the family Mesosauridae (Reptilia: Proganosauria) with special reference to its associated fauna and palaeoecological environment in the Whitehill sea.* Unpublished PhD thesis, University of Stellenbosch, Stellenbosch.
OELOFSEN, B.W. 1987. The biostratigraphy and fossils of the Whitehill and Irati Shale formations of the Karoo and Paraná basins. *Geophysical Monograph* **41**, 131–138.
OLSEN, P.E. & GALTON, P.M. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia africana* **25**, 87–110.
OLSON, E.C. & BROOM, R. 1937. New genera and species of tetrapods from the Karroo beds of South Africa. *Journal of Paleontology* **11**, 613–619.
OLSEN, E.C. & LAMMERS, G.E. 1976. A new brachyopoid amphibian. **In**: Churcher, C.S. (ed.), *Athlon: Essays in Paleontology in Honour of Loris Shano Russell,* 45–57. Toronto, The University of Toronto press.
OWEN, R. 1876a. On *Petrophryne granulata* Ow., a labyrinthodont reptile from the Trias of South Africa, with special comparison of the skull with that of *Rhinosaurus jasikovii* Fisch. *Bulletin de la Société Impériale des Naturalistes de Moscou* **50**, 147–153.
OWEN, R. 1876b. *Catalogue of the Fossil Reptiles of South Africa.* London, British Museum (Natural History).
OWEN, R. 1884. On a labyrinthodont amphibian (*Rhytidosteus capensis*) from the Trias of the Orange Free State, Cape of Good hope. *Quarterly Journal of the Geological Society* **40**, 333–338.
PARRINGTON, F.R. 1948. Labyrinthodonts from South Africa. *Proceedings of the Zoological Society* **118**, 426–445.
ROMER, A.S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard College* **99**, 1–352.
ROMER, A.S. 1975. Intercontinental correlations of Triassic Gondwana vertebrate faunas. **In:** Campbell, K.S.W. (ed.), *Gondwana Geology: Papers from the Third Gondwana Symposium,* 469–473. Canberra, Australian National University Press.
RUBIDGE, B.S. 1995. *Biostratigraphy of the Beaufort Group (Karoo Supergroup).* South African Committee for Stratigraphy Biostratigraphic Series No. 1. Pretoria, Council for Geoscience.
RUBIDGE, B.S., HANCOX, P.J. & CATUNEANU, O. 2000. Sequence analysis of the Ecca–Beaufort contact in the southern Karoo of South Africa. *South African Journal of Geology* **103**, 81–96.
RUSCONI, C. 1949. Otra especie de Labyrintodonte del Triásico de Mendoza. *Revista del Museo de Historia Natural de Mendoza* **3**, 93–94.
SCHOCH, R.R. & MILNER, A.R. 2000. *Stereospondyli.* Handbuch der Paläoherpetologie, Teil 3B. München, Verlag Dr. Friedrich Pfeil.
SEELEY, H.G. 1907. Evidences of a mandible of a new labyrinthodont from the Upper Karroo Beds of Cape Colony (*Ptychosphenodon browni*). *Geological Magazine* **4**, 433–436.
SEELEY, H.G. 1908. A large labyrinthodont tooth from the Upper Karroo

Beds of Wonderboom, near Burghersdorp. *Geological Magazine* **5**, 241–243.
SHISHKIN, M.A. 1960. *Inflectosaurus amplus,* a new Triassic trematosaurid. *Palaontologicheskiy Zhurnal* **1960**, 130–148 (in Russian).
SHISHKIN, M.A. 1961. New data on *Tupilakosaurus. Doklady Akademii Nauk SSSR* **136**, 938–941.
SHISHKIN, M.A. 1964. Stereospondyli. **In**: Orlov, I.A. (ed.), *Fundamentals of Palaeontology: Amphibians, Reptiles and Birds,* 83–122. Moscow, Nauka (in Russian).
SHISHKIN, M.A. 1980. The Luzocephalidae, a new Triassic labyrinthodont family. *Paleontological Journal* **14**, 88–100.
SHISHKIN, M.A. 1991. A Late Jurassic labyrinthodont from Mongolia. *Paleontological Journal* **25**, 78–91.
SHISHKIN, M.A. 1994. A Gondwanan rhytidosteid (Amphibia, Temnospondyli) from the Lower Triassic of southern Cis-Uralia. *Paleontological Journal* **28**, 127–143.
SHISHKIN, M.A. 2000. Olenekian-Anisian boundary in the history of land tetrapods. **In**: Gradinaru, E. (ed.), *Workshop on the Lower-Middle Triassic (Olenekian-Anisian) Boundary,* 7–10 June, Tulcea, Romania, 60–69.
SHISHKIN, M.A. & RUBIDGE, B.S. 2000. A relict rhinesuchid (Amphibia: Temnospondyli) from the Lower Triassic of South Africa. *Palaeontology* **43**, 653–670.
SHISHKIN, M.A., RUBIDGE, B.S. & HANCOX, P.J. 1995. Vertebrate biozonation of the Upper Beaufort Series of South Africa – a new look on correlation of the Triassic biotic events in Euramerica and southern Gondwana. **In**: Sun, A. & Wang, Y. (eds), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers, 1995,* 39–41. Beijing, China Ocean Press.
SHISHKIN, M.A., RUBIDGE, B.S. & KITCHING, J.W. 1996. A new lydekkerinid (Amphibia, Temnospondyli) from the lower Triassic of South Africa: implications for evolution of the early capitosauroid cranial pattern. *Philosophical Transaction of the Royal Society of London B* **351**, 1635–1659.
SHISHKIN, M.A. & WELMAN, J. 1994. A new find of *Trematosuchus* (Amphibia, Temnospondyli) from the *Cynognathus* Zone of South Africa. *Palaeontologia africana* **31**, 39–49.
SMITH, R.M.H. 1990. A review of stratigraphy and sedimentary environments of the Karoo Basin of South Africa. *Journal of African Earth Sciences* **10**, 117–137.
SMITH, R.M.H. 1995. Changing fluvial environments across the Permian–Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **117**, 81–104.
SMITH, R.M.H. & KITCHING, J.W. 1997. Sedimentology and vertebrate taphonomy of the *Tritylodon* Acme Zone: a reworked paleosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **131**, 29–50.
TRUEB, L. & CLOUTIER, R. 1991. A phylogenetic investigation of the inter- and intra-relationships of the Lissamphibia (Amphibia, Temnospondyli). **In:** Schultze, H.P. & Trueb, L. (eds), *Origins of the Higher Groups of Tetrapods – Controversy and Consensus,* 223–313. Ithaca, Cornell University Press.
VAN HEERDEN, J. 1974. A short note on some natural casts of the cotylosaurian reptile *Procolophon*. *Navorsinge van die Nasionale Museum* **2**, 417–428.
VAN HOEPEN, E.C.N. 1911. Korte, voorlopige beschrijving van te Senekal gevonden Stegocephalen. *Annals of the Transvaal Museum* **3**, 102–106.
VAN HOEPEN, E.C.N. 1915. Stegocephalia of Senekal, O.F.S. *Annals of the Transvaal Museum* **5**, 125–149.
VAN HOEPEN, E.C.N. 1917. Note on *Myriodon* and *Platycranium. Annals of the Transvaal Museum* **5**, 217.
WARREN, A.A. 1980. *Parotosuchus* from the Early Triassic of Queensland and Western Australia. *Alcheringa* **4**, 25–36.
WARREN, A.A. 1998. *Laidleria* uncovered: a redescription of *Laidleria gracilis* Kitching (1957), a temnospondyl from the *Cynognathus* Zone of South Africa. *Zoological Journal of the Linnean Society* **122**, 167–185.
WARREN, A.A. 1999. Karoo tupilakosaurid: a relict from Gondwana. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **89**, 145–160.
WARREN, A.A. & BLACK, T. 1985. A new rhytidosteid (Amphibia, Labyrinthodontia) from the Early Triassic Arcadia Formation of Queensland, Australia, and the relationships of Triassic temnospondyls. *Journal of Vertebrate Paleontology* **5**, 303–327.
WARREN, A.A. & DAMIANI, R.J. 1999. Stereospondyl amphibians from the Elliot Formation of South Africa. *Palaeontologia africana* **35**, 45–54.
WARREN, A.A., DAMIANI, R.J. & YATES, A.M. 2000. Palaeobiogeography of Australian fossil amphibians. *Historical Biology* **15**, 171–179.
WARREN, A.A. & HUTCHINSON, M.N. 1990. *Lapillopsis,* a new genus of temnospondyl amphibians from the Early Triassic of Queensland. *Alcheringa* **14**, 149–158.
WATSON, D.M.S. 1912. On some reptilian lower jaws. *Annals and Magazine of Natural History* **10**, 573–587.
WATSON, D.M.S. 1913. *Micropholis stowi,* Huxley, a temnospondylous amphibian from South Africa. *Geological Magazine* (Decade V) **10**, 340–346.
WATSON, D.M.S. 1919. The structure, evolution and origin of the Amphibia. The 'Orders' Rachitomi and Stereospondyli. *Philosophical Transaction of the Royal Society of London B* **209**, 1–73.
WATSON, D.M.S. 1956. The brachyopid labyrinthodonts. *Bulletin of the British Museum (Natural History), Geology* **2**, 315–392.
WATSON, D.M.S. 1962. The evolution of the labyrinthodonts. *Philosophical Transaction of the Royal Society of London B* **245**, 219–265.
WELLES, S.P. 1993. A review of the lonchorhynchine trematosaurs (Labyrinthodontia), and a description of a new genus and species from the Lower Moenkopi Formation of Arizona. *PaleoBios* **14**, 1–24.
WELLES, S.P. & COSGRIFF, J.W. 1965. A revision of the labyrinthodont family Capitosauridae and a description of *Parotosaurus peabodyi,* n. sp. from the Wupatki Member of the Moenkopi Formation of Northern Arizona. *University of California Publications in Geological Sciences* **54**, 1–148.
WELLES, S.P. & ESTES, R. 1969. *Hadrokkosaurus bradyi* from the Upper Moenkopi Formation of Arizona with a review of the brachyopid labyrinthodonts. *University of California Publications in Geological Sciences* **84**, 1–61.
WERNEBURG, R. & SCHNEIDER, J. 1996. The Permian temnospondyl amphibians of India. *Special Papers in Palaeontology* **52**, 105–128.
YATES, A.M. & WARREN, A.A. 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* **128**, 77– 121.
ZITTEL, K.A. von 1887–1890. *Handbuch der Paläontologie. Abteilung 1. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves).* Munich and Leipzig, Oldenbourg.
ZITTEL, K.A. von 1923. *Grundzüge der Paläontologie (Paläozoologie). II. Vertebrata.* Munich and Berlin, Oldenbourg.