

The South African stereospondyl *Lydekkerina huxleyi* (Tetrapoda, Temnospondyli) from the Lower Triassic of Australia

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Abstract – The first tetrapod fossil from the Rewan Formation of the Galilee Basin, central Queensland, Australia, is identified as *Lydekkerina huxleyi*, a stereospondyl found elsewhere only in the *Lystrosaurus* Assemblage Zone of South Africa. Apomorphies shared with *L. huxleyi* are: anterior palatal vacuity with anterodorsal projections from its posterior margin; ventral surface of skull roof with series of thickened ridges (condition unknown in other lydekkerinids); and vomerine shagreen present (possible autapomorphic reversal). Restudy of the only other Australian lydekkerinid, *Chomatobatrachus halei*, shows it to be distinct from *L. huxleyi*. The Rewan Formation, undifferentiated in the Galilee Basin, can be correlated with the Rewan Group of the Bowen Basin, and to the early part of the *Lystrosaurus* Assemblage Zone of the Karoo Basin, South Africa, which are of Griesbachian age. Varying palaeoenvironments may contribute to the contrasting nature of the Australian and South African faunas.

Keywords: Early Triassic, *Lydekkerina*, Australia, Arcadia Formation, *Lystrosaurus* Assemblage Zone.

1. Introduction

In Australia, Early Triassic stereospondyl (Tetrapoda, Temnospondyli) faunas are known from the Arcadia Formation (Rewan Group; Bowen Basin) of Queensland, the Knocklofty Formation (Tasmania Basin) of Tasmania, the Blina Shale (Canning Basin) of Western Australia, and the Narrabeen Group (Sydney Basin) of New South Wales. Among these, the Arcadia Formation has the greatest diversity of stereospondyls but to date has not yielded an identifiable member of the Lydekkerinidae, although this taxon was previously reported as present (Warren, 1980). *Chomatobatrachus halei* from the Knocklofty Formation, based on a collection of skulls, mandibles, and postcranial material, is the only described lydekkerinid from Australia (Cosgriff, 1974). The specimen described below, collected in 1991 by Dr Tony Thulborn and the late Tim Hamley, is the first tetrapod from the Rewan Formation of the Galilee Basin, and the second lydekkerinid from Australia.

Elsewhere in Pangaea the Lydekkerinidae have been described from the lower part of the Lower Triassic of Antarctica (Colbert & Cosgriff, 1974), India (Tripathi, 1969), Russia and Greenland (Shishkin, 1980), and Madagascar (Swinton, 1956; Hewison, 1996). By far the most common and best known lydekkerinids, however, are from the *Lystrosaurus* Assemblage Zone

of the Beaufort Group, Karoo Basin, South Africa. In a review of the genus *Lydekkerina*, based on a redescription of the newly prepared holotype of *L. huxleyi*, BMNH R507 (Jeannot, Damiani & Rubidge, in press), two South African taxa were recognized: *L. huxleyi*, known from over 250 specimens, and *Eolydekkerina magna* (Shishkin, Rubidge & Kitching, 1996). *Lydekkerina huxleyi* is thus the best-known lydekkerinid. Despite this, the taxon is difficult to diagnose, with only three autapomorphies recognized by Jeannot, Damiani & Rubidge (in press).

The new lydekkerinid from the Rewan Formation of the Galilee Basin in central Queensland is identified as *Lydekkerina huxleyi*, the first specimen to be found outside South Africa. This has implications for the age assessment and, in particular, correlation of the Rewan Formation and Arcadia Formation fauna, as will be discussed in Section 5.

2. Material and methods

QMF 39705 consists of a skull preserved in partial articulation with remains of the left and right mandibles. Most of the skull roof is represented by an impression of the ventral surface. The specimen was prepared mechanically using an ARO engraver and carbide rods in a pin vice. Repositories for specimens, and abbreviations used in the text, are indicated by the following prefixes: BMNH – Natural History Museum, London; BMR – Bureau of Mineral Resources, Geology and Geophysics; GSQ – Geological Survey of Queensland; QML – Queensland Museum Locality; QMF – Queensland Museum Fossil;

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3. Systematic palaeontology

TEMNOSPONDYLI Zittel, 1887–1890

STEREOSPONDYLI Zittel, 1887–1890

LYDEKKERINIDAE Watson, 1919

Revised diagnosis. Distinguished from all other stereospondyls by the following combination of characters. Sympletiomorphies: sensory sulci weakly impressed and discontinuous; frontals excluded from orbital margins; crista falciformis of squamosal absent; denticle fields present on pterygoids and parasphenoid; tubera parasphenoidales bordered by deeply excavated ‘pockets’ which pass onto the side wall of the exoccipitals; ventral pterygoid crest present; denticle fields present on anterior, middle and posterior coronoids. Synapomorphies: step-shaped lacrimal flexure of the infraorbital sulcus; step-shaped contact between the nasal and prefrontal; slight indentation of anterolateral margin of interpterygoid vacuity; crista tympanica of the squamosal present; cheek margin straight in occipital view. Diagnosis after Jeannot, Damiani & Rubidge (in press).

Lydekkerina huxleyi (Lydekker) Broom, 1915

Bothriceps huxleyi Lydekker, 1889

Lydekkerina huxleyi (Lydekker) Broom, 1915

Putterillia platyceps Broom, 1930

Lydekkerina dutoiti Broom, 1930

Broomulus dutoiti (Broom) Romer, 1947

Limnoiketes paludinatans Parrington, 1948

Revised diagnosis. *Lydekkerina huxleyi* can be distinguished from all other lydekkerinids by the following autapomorphic characters: anterior palatal vacuity with anterodorsal projections from its posterior margin; ventral surface of skull roof with series of thickened ridges (condition unknown in other lydekkerinids); vomerine shagreen present (possible autapomorphic reversal). Diagnosis after Jeannot, Damiani & Rubidge (in press).

Locality and horizon. The new material (QMF 39705) comes from Alpha property, QML 1434, approximately 50 km south of the town of Alpha, Queensland (Fig. 1). The locality lies in the southeastern part of the Galilee Basin, immediately adjacent to the Springsure Shelf area of the Bowen Basin. Triassic rocks in the Bowen Basin were extended to the Galilee Basin having been mapped across the Springsure Shelf (e.g. Exon *et al.* 1972). The locality is lower Rewan Formation (Exon, 1970) and is probably Griesbachian, or possibly Changhsingian in age (Fig. 2). Sedimentary strata are pale buff to yellow fine-grained sandstones and mudstones, unlike the typical red and yellow to green, striped sedimentary rocks of the upper Rewan Group (Arcadia Formation) in the Bowen Basin.

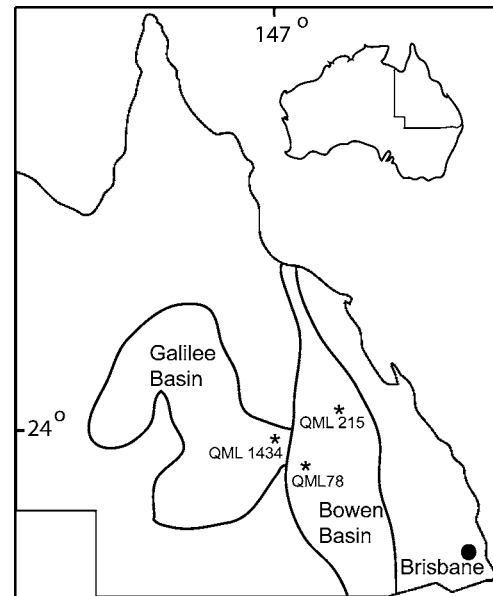


Figure 1. Locality map showing the two principle vertebrate localities (QML 78 and QML 215) in the Arcadia Formation of the Rewan Group, Bowen Basin, Queensland, Australia, and the new locality (QML 1434) in the Rewan Formation of the Galilee Basin.

| Chronostratigraphy | | | SE Galilee Basin | SW Bowen Basin | Karoo Basin |
|--------------------|---------------|-------------|-------------------|-------------------|------------------------|
| Period | Stage | Spore Units | | | |
| Early Triassic | Spathian | APT2 | Clematis Sst. | Glenidal Fm. | <i>Cynognathus</i> AZ |
| | Nammalian | | Dunda Beds | Arcadia Fm. | <i>Lystrosaurus</i> AZ |
| | Griesbachian | APT1 | Rewan Fm. | Sagittarius Sst. | |
| Late Permian | Changhsingian | APP6 | Bandanna Fm. | Bandanna Fm. | |
| | Wuchiapingian | APP5 | Black Alley Shale | Black Alley Shale | |
| | | | | | |

Figure 2. Stratigraphic correlation chart showing the approximate position (marked by tetrapod symbol) of the new locality in the Rewan Formation of the southeastern Galilee Basin in relation to the vertebrate faunas in the Arcadia Formation of the southwestern Bowen Basin and the *Lystrosaurus* Assemblage Zone of the Karoo Basin (South Africa). Permian assemblage zones of the Karoo Basin are not included. Spore Units after Price (1997). Abbreviations: AZ – Assemblage Zone; Fm. – Formation; Sst. – Sandstone.

4. Description

4.a. Skull

Most of the skull roof preserved (Fig. 3a) is an impression of the inner surface of the dermal bones but some outer surface remains around the right external nostril, posterior to the left orbit, to the left of the pineal foramen, and on the labial surface of the anterior part of the right mandible. These surfaces carry typical

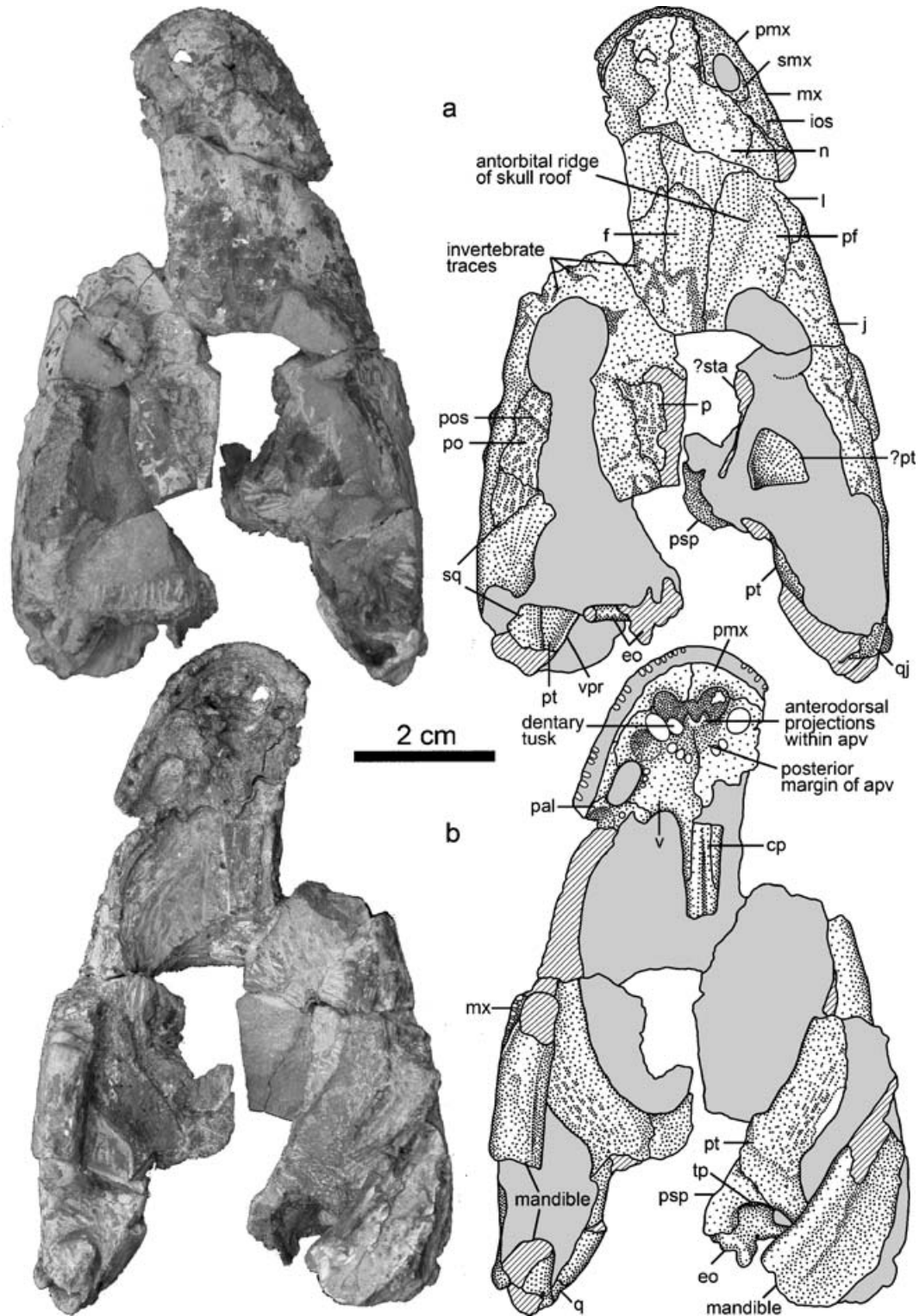


Figure 3. The temnospondyl *Lydekkerina huxleyi* QMF 39705, from the Rewan Formation of the Galilee Basin, Queensland, Australia. (a) dorsal view of the skull; (b) ventral view of the skull. Note the triangular depression behind the anterior palatal vacuity, and part of the right dentary tusk in (b). Abbreviations used in Figures 3 and 4: apv – anterior palatal vacuity; ch – choana; cp – cultriform process of the parasphenoid; ect – ectopterygoid; eo – exoccipital; f – frontal; ios – infraorbital sulcus; j – jugal; l – lacrimal; mx – maxilla; n – nasal; nf – nutritive foramen; p – parietal; pal – palatine; pf – prefrontal; pmx – premaxilla; po – postorbital; pof – postfrontal; pop – paroccipital process; pos – postorbital sulcus; pp – postparietal; pt – pterygoid; ?pt – cone-shaped flange of bone disassociated from the pterygoid; psp – parasphenoid; q – quadrate; qj – quadratojugal; smx – septomaxilla; sos – supraorbital sulcus; sq – squamosal; st – supratemporal; ?sta – stapes; t – tabular; tp – tubera parasphenoidales; ts – temporal sulcus; v – vomer; vpr – ventral pterygoid ridge; IX-X – foramen for nerves IX-X.

lydekkerinid pitted ornament, while weakly impressed sensory canals traverse the ornament below the right nostril and behind the left orbit. Those parts of the palate preserved (Fig. 3b) are of bone rather than bone impression. The skull roof measures approximately 90 mm midline length by 65 mm maximum breadth, a little narrower than most South African specimens, and may have been slightly laterally compressed.

Several areas of matrix beneath the skull roof impressions are excavated by irregular traces that appear to be invertebrate burrows, preserved in concave epirelief (Bromley, 1990, p. 165). These are often elongate, sometimes branched and, in one case, a burrow connects with another beneath the surface. Such an invertebrate may have been feeding on the tissue beneath the skull roof immediately after the fossil was buried in sediment. On the skull roof impression, slight indentations pass anterolaterally in front of the right orbit and posterolaterally behind the left orbit, corresponding (in part) to the thickened ridges on the ventral surface of the skull roof found in *Lydekkerina huxleyi* (Jeannot, Damiani & Rubidge, in press).

The right external nostril and choana, both orbits, the anterior palatal vacuity, and right interpterygoid and both subtemporal vacuities are preserved. The usual stereospondyl complement of cranial and palatal dermal bones are present, although some sutures are hard to determine. On the dermal skull roof, a small septomaxilla lies posterior to the right external nostril. On the left, the maxilla is broken posteriorly, with the cross-section suggesting a posterior extension along the interpterygoid vacuity. Jeannot, Damiani & Rubidge (in press) suggested that this unusually long posterior extension of the maxilla could be diagnostic of the Lydekkerinidae.

On the palatal surface (Fig. 3b), ornament is evident on the palatal ramus of the pterygoids while patches of denticles (shagreen) are present on the vomers, the cultriform process of the parasphenoid, and the body and palatal ramus of the pterygoids. Overall the denticles are poorly preserved or present as basal sections.

The anterior palatal vacuity has been prepared as far as the skull roof. It is reniform in that a midline projection of the premaxillae interrupts the anterior border. Posteriorly and ventrally, a median embayment extends the posterior margin of the vacuity, making the margin 'pointed' (Schoch & Milner, 2000); however, this embayment is only present superficially, with deeper layers of the vomers showing a rounded margin to the vacuity. Extending these deep layers anteriorly are paired projections, first described in *Lydekkerina huxleyi* from South Africa, and thought to be autapomorphic for that species (Jeannot, Damiani & Rubidge, in press).

The remains of the parasphenoid basal plate suggest that it was not elongate, in contrast to *Chomatobatrachus halei* (Cosgriff, 1974; Jeannot, Damiani &

Rubidge, in press). A deep crista muscularis (=tubera parasphenoidales of Clack & Holmes, 1988) is preserved on the left, extending onto the ventral surface of the exoccipital, as is typical of *Lydekkerina huxleyi* from South Africa. The right side of the exoccipital occupies a broad band posterior to the body of the parasphenoid as in the South African lydekkerinids, in which the exoccipitals apparently fuse in the midline; in most stereospondyls, paired exoccipitals taper towards the posterior midline. Watson (1919) suggested that the exoccipitals of *L. huxleyi* were bridged by a ventral exposure of the basioccipital, but no sutures are visible in this area.

In occipital view, a ventral pterygoid crest (Jeannot, Damiani & Rubidge, in press), labelled 'memb' by Watson (1962), is present on the ascending flange of the left quadrate ramus of the pterygoid. The ventral pterygoid crest is not homologous with the crista obliqua of mastodonsauroids, as argued by Jeannot, Damiani & Rubidge (in press). On the right, a thin, cone-shaped flange of bone may have been displaced anteriorly from the right pterygoid. This structure resembles the posterior face of the inner part of the ascending ramus of the pterygoid in brachyopoids. The internal structure of the skull is unknown in *Lydekkerina huxleyi*. A small part of a crista tympanica squamosi, thought to be typical of lydekkerinids and rhinesuchids (Shishkin, Rubidge & Kitching, 1996), is preserved on the left. A probable partial stapes with a robust footplate and slender shaft is preserved on the right, just anterior to the cone-shaped structure (above). This element could also be an epipterygoid, an element undescribed to date in *Lydekkerina* from South Africa.

4.b. Mandible

Three sections of the right mandible are preserved, two in partial articulation, as well as a posterior portion of the left mandible (Fig. 3b). The anterior section of the right mandible, which is preserved isolated from the skull, begins at the symphysis and includes parts of the dentary, splenial and anterior coronoid. A more posterior section of mandible includes the posterior part of the dentary and posterior coronoid, and parts of the angular, prearticular and surangular (including the posterior meckelian foramen), while the most posterior section is part of the prearticular (including the chorda tympanica foramen) and articular. The left mandible preserves parts of the surangular and posterior coronoid, and some dentary teeth.

4.c. Dentition

Marginal teeth on the maxilla and dentary are approximately of equal size and do not decrease in size posteriorly as far as they are preserved. Individual teeth are slim, sub-rounded at the base and curve inwards towards their tips. Tusks are present on the vomers and

the remains of a tusk and a tusk pit are present on the right palatine, but the tooth-bearing margin of the ectopterygoid is concealed by a part of the mandible. An arcuate tooth row is poorly preserved immediately posterior to the anterior palatal vacuity.

On the mandible few teeth are preserved. A dentary tusk and tusk pit are present but there is no parasymphyseal tooth row. Both posterior coronoids have uneven rows of large denticles, with individual denticles approaching the size of adjacent maxillary teeth. The small portion of the right anterior coronoid is badly preserved so that the presence of anterior coronoid teeth is not determinable.

5. Discussion

5.a. Taxonomic position

The immediate identification of QMF 39705 as *Lydekkerina huxleyi* was facilitated by further preparation of the holotype of *L. huxleyi* (BMNH R507) at the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, and its further description by Jeannot, Damiani & Rubidge (in press). QMF 39705 is clearly a member of the Lydekkerinidae using the revised diagnosis and shares all three autapomorphies of *L. huxleyi* identified by those authors.

QMF 39705 can be differentiated from *Chomatobatrachus halei* (Cosgriff, 1974), the only other Australian lydekkerinid (Fig. 4), by the following characters. *Chomatobatrachus* has a premaxilla that is elongated anterior to the nares (Fig. 4a, b), an anterolateral process of the palatine that almost contacts a posterolateral process of the vomer (thereby reducing the maxillary contribution to the choana), a longer parasphenoid plate, a transvomerine tooth row that is displaced posteriorly in the adult, and lacks the paired anterodorsal projections of the anterior palatal vacuity (Fig. 4c). Cosgriff (1974, p. 48) noted that the posterior margin of the anterior palatal vacuity of *C. halei* was 'invaded by irregular, poorly ossified projections of the vomer bones'. These are quite unlike the processes in *Lydekkerina huxleyi*, resembling posterolateral shelves of bone rather than more medial projections. In addition to these characters, the holotype of *L. huxleyi* differs from *C. halei* because *C. halei* has a more fully expressed lateral line system, and no postparietal lappets.

The unusual triangular shape of the nostril in *Chomatobatrachus halei* suggests that the septomaxilla has fallen out, as often occurs in *Lydekkerina huxleyi* (Jeannot, Damiani & Rubidge, in press). There are indications that the palate of *C. halei* may have been more denticulate than in *L. huxleyi* as the palate of the juvenile specimens (Fig. 4e) has patches of denticles preserved on the palatine and ectopterygoid, in addition to the usual pterygoid and parasphenoid shagreen.

Denticulate areas are poorly preserved in the adult. Previous suggestions that the mandible referred by Cosgriff (1974) to *C. halei* may not be lydekkerinid (Warren & Black, 1985; Jupp & Warren, 1986) were based in part on the extensive cover of denticles which was thought to be a rhytidosteid character. We suggest that this allocation may not be correct in light of the denticle cover in the juvenile *C. halei*.

5.b. Stratigraphic position

The Rewan Formation in the Bowen Basin was elevated to group status by Jensen (1975), who divided it into a lower Sagittarius Sandstone and, in conformable contact, an upper Arcadia Formation, with the base of the Sagittarius Sandstone lying just above the youngest coal. Jensen assumed that the Rewan Group began at the Permo-Triassic boundary and this position has been followed by others (e.g. Grech & Dyson, 1997). In these studies, the Sagittarius Sandstone would be lowest Triassic age, with the Arcadia Formation later in the Scythian. However, evidence from microflora suggests that the base of the Rewan Group, and much of the Sagittarius Sandstone, is of Permian age (e.g. Foster, 1982; Foster & Jones, 1994). This position was adopted in an overview of Australian Phanerozoic stratigraphy based largely on SHRIMP dating (Archbold & Dickens, 1996), and supported by U/Pb age data on zircons (Mundil *et al.* 2002).

The precise position of the Permo-Triassic boundary in Australia remains elusive, being situated somewhere between two anchor points: in eastern Australia, palynological evidence correlates the earliest part of the Rewan Group with the early part of the Changhsingian (Late, but not latest, Permian), while the late Early Triassic is defined by marine faunas in Western Australia (Foster, Logan & Summons, 1998). If we accept the evidence that the lower part of the Rewan Group, that is, part or all of the Sagittarius Sandstone, is Permian, then the upper part of the Rewan Group (the Arcadia Formation) must lie close to the base of the Triassic (Fig. 2).

It is difficult to determine with certainty the stratigraphic position of the two main vertebrate faunas from QML 78 and QML 215 (e.g. Warren, 1980) within the Arcadia Formation. Originally, Jensen (pers. comm. 1969) suggested that the fauna from QML 78, in the southwestern part of the Bowen Basin, was 'lower, upper Rewan Group', that is, lower Arcadia Formation, and that 'the position of QML 215 was similar'. This position was misquoted in several later papers as lower upper Arcadia Formation (e.g. Warren, 1981). Nevertheless, a Griesbachian age for the Arcadia Formation fauna has been adopted by most palaeontologists (Warren, 1980; Thulborn, 1983, 1986; McLoughlin, Lindström & Drinnan, 1997), but not Battail (1988), who hypothesized that it was Smithian. The fauna was positioned on the Griesbachian–Nammalian boundary

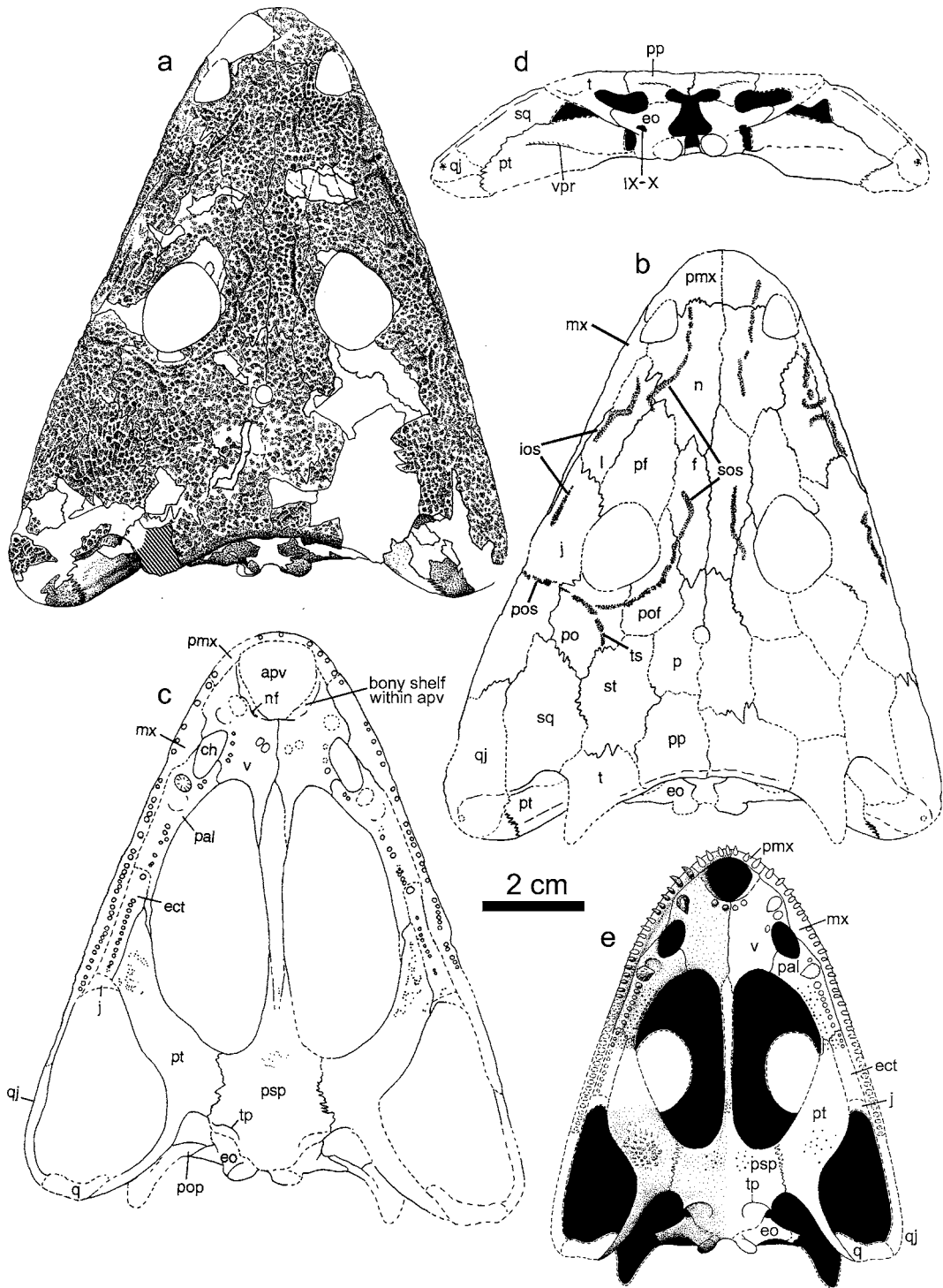


Figure 4. The temnospondyl *Chomatobatrachus halei*, from the Knocklofty Formation of the Tasmania Basin, Australia. (a) Dorsal view of skull roof of UTGD 80738 (holotype) as preserved; (b–d) reconstructions of skull of UTGD 80738 in (b) dorsal, (c) ventral and (d) occipital views; (e) composite reconstruction of a juvenile skull in ventral view, based on UTGD 87791 and UTGD 87792. Note the bony shelves on the lateral margins of the anterior palatal vacuity, the denticulate palatine and ectopterygoid in the juvenile, and the transvomerine tooth row which follows the posterior border of the anterior palatal vacuity in the juvenile but not in the adult.

by Balme & Foster (1996). In an overview of the stratigraphic relationships of the vertebrate fauna from all Australian Lower Triassic sites using all available evidence, Northwood (C. Northwood, unpub. Ph.D. thesis, La Trobe Univ., 1997) correlated the level of the vertebrate fauna within the Arcadia Formation with the

APT1 *Lunatisporites pellucidus* zone, that is, earliest Triassic (Griesbachian, lower Induan).

In the Galilee Basin, the Rewan Formation was not subdivided (Exon, 1970) and its stratigraphic position is not well defined. In the northern part of the Galilee Basin, it conformably overlies the Permian Blackwater

Group (Betts Creek Beds) that contains tuff beds probably equivalent to the Burngrove Formation that underlies the Rangol Coal Measures in the Bowen Basin (Hawkins *et al.*, Geology and resource potential of the northern Galilee Basin, unpub. manuscript). The Rewan Formation thus extends down into the Permian. Further, in the northern part of the Galilee Basin, both Permian (APP6) and earliest Triassic (APT1) miospores have been identified in the Rewan Formation in GSQ Muttaborra 1 (McKellar, 1991). In the southeastern Galilee Basin, BMR Tambo 34, sited on Alpha property close to QML 1434, was considered Tr2a (Exon *et al.* 1972) and contains *Taeniaesporites* but lacks *Aratrisporites*, indicating assignment to APT1 (J. McKellar, pers. comm. 2004).

Division of the Rewan Formation in the Galilee Basin into a Late Permian and an Early Triassic component is thus similar to the division in the Bowen Basin. If *Lydekkerina huxleyi* is confined to Triassic strata as it is in South Africa (Fig. 2), then it is most likely to be from the upper part of the Rewan Formation in the Galilee Basin, that is, in a similar stratigraphic position to the Arcadia Formation vertebrate fauna of the Bowen Basin.

The Knocklofty Formation of Tasmania, containing the other Australian lydekkerinid, *Chomatobatrachus halei*, was shown to be Griesbachian or Nammalian on the basis of contained spores (Banks & Naqvi, 1967). Therefore, both Australian faunas that contain lydekkerinid stereospondyls are of a similar age, that is, earliest Triassic.

5.c. Faunal correlation

In the *Lystrosaurus* Assemblage Zone *Lydekkerina huxleyi* is by far the most common stereospondyl, and is found through all but the upper reaches of that biozone (Damiani, 2004), which extends from the base of the Triassic (Induan) to the end of the lower Olenekian (Hancox, 2000; Neveling, 2004). The presence of *L. huxleyi* in the Rewan Formation of the Galilee Basin allows for correlation of that formation with the *Lydekkerina*-bearing part of the *Lystrosaurus* Assemblage Zone. By implication, the Arcadia Formation fauna is of equivalent age to the *Lydekkerina*-bearing part of the *Lystrosaurus* Assemblage Zone, and, following the arguments above, from near the base of that biozone.

The described vertebrate fauna from the Arcadia Formation is consistent with an earliest Triassic age. It includes an assemblage of stereospondyls that are in most cases plesiomorphic members of their clades: *Lapillopsis* (a stem stereospondyl: Yates, 1999); *Watsonisuchus* (Mastodontosauridae: Damiani, 2001); *Keratobrachyops* (Chigutisauridae: Warren, 1981); *Xenobrachyops* (Brachyopidae: Howie, 1972) and *Arcadia* and *Acerastea* (Rhytidosteiidae: Warren & Black, 1985; Warren & Hutchinson, 1988). These

stereospondyls, with the exception of *Watsonisuchus* (Damiani, Neveling & Hancox, 2001), are not represented in the *Lystrosaurus* Assemblage Zone of South Africa, where *L. huxleyi* is common. The reptilian taxa from the Arcadia Formation are, however, more typical of the South African *Lystrosaurus* Assemblage Zone forms, and include a primitive procolophonoid (possibly an owenettid: S. Evans, pers. comm. 2004), *Kadimakara* (Bartholomai, 1979), which may be congeneric with *Prolacerta* (S. Evans, pers. comm. 2004), and *Kalisuchus* (Thulborn, 1979), an early archosauromorph related to *Proterosuchus*. Outstanding in the Arcadia fauna is the preponderance of stereospondyls compared to reptiles and the virtual absence of the commonest components of the *Lystrosaurus* Assemblage Zone fauna: *Lystrosaurus* was identified from a few fragments of dicynodont only (King, 1983; Thulborn, 1983), while the identification of lydekkerinids (Warren, 1980) rests on a few pieces of scrap bone.

In summary, the presence of *Lydekkerina huxleyi* in the Galilee Basin indicates that part of the Rewan Formation is equivalent in age to the *Lystrosaurus* Assemblage Zone of South Africa. A microfloral age of APT1, the earliest Triassic, for the Rewan Formation in the southeastern Galilee Basin, suggests a correlation with the lowermost part of the *Lystrosaurus* Assemblage Zone. This position adds weight to previous deductions that the Arcadia Formation fauna from the adjacent Bowen Basin is from the earliest Triassic (Griesbachian).

5.d. Palaeoenvironment

As currently defined, the *Lystrosaurus* Assemblage Zone is encompassed by three lithostratigraphic units in the main Karoo Basin of South Africa: the Palingkloof Member (which is the uppermost member of the Balfour Formation), the Katberg Formation and the lower third of the Burgersdorp Formation (Groenewald & Kitching, 1995). However, based on extensive regional research, Neveling (2004) restricted the *Lystrosaurus* Assemblage Zone to the Palingkloof Member and the Katberg Formation only. The Permo-Triassic boundary coincides with a distinctly laminated mudrock horizon within the Palingkloof Member (Ward, Montgomery & Smith, 2000; Retallack, Smith & Ward, 2003, and references cited therein). The Palingkloof Member reaches a maximum thickness of 100 m and comprises mainly red and maroon mudstones with subordinate sandstones, broadly representing high sinuosity channel and floodplain deposits that accumulated under semi-arid climatic conditions (Smith, 1995; G. H. Groenewald, unpub. Ph.D. thesis, Univ. Port Elizabeth, 1996). The overlying Katberg Formation reaches a maximum thickness of 1000 m and thus forms the bulk of the *Lystrosaurus* Assemblage Zone strata. It comprises mainly stacked,

tabular sheets of fine- to medium-grained sandstones, with subordinate red and greenish-grey mudstones, and is considered to have been deposited by a low-sinuosity, braided river system under dry climatic conditions (Hiller & Stavrakis, 1984; Smith, 1995; Groenewald & Kitching, 1995; G. H. Groenewald, unpub. Ph.D. thesis, Univ. Port Elizabeth, 1996; Neveling, 2004). Fossils in the *Lystrosaurus* Assemblage Zone are locally abundant within the interchannel mudrocks and are often found as clusters of complete or near-complete skulls and skeletons encased in calcareous nodules (Smith, 1995). This mode of preservation may have been facilitated by increasingly arid conditions on the floodplains on which the dry-adapted *Lystrosaurus* Assemblage Zone fauna flourished (Smith, 1995).

In contrast, the Arcadia Formation of the Bowen Basin consists dominantly of red-brown massive mudstones which form thick sequences of overbank deposits, interbedded with lesser, well-defined channel sandstones (Jensen, 1975; Kassan & Fielding, 1996). Deposition of the Arcadia Formation strata occurred via meandering and anastomosing river systems onto large, vegetated alluvial plains under climatic conditions that were warm to subarid with strongly seasonal rainfall (Cantrill & Webb, 1998).

The distinctive nature of the Arcadia Formation fauna, namely the dominance of aquatic stereospondyls and the paucity of dicynodont and reptile remains, coupled with its geographically isolated location on the tip of the eastern Gondwanan peninsula (Thulborn, 1986), suggests that the local environment of deposition may have been distinct from those with faunas dominated by *Lystrosaurus*. Specifically, the Arcadia Formation may be sampling a comparatively wet floodplain habitat, in contrast to the dry floodplains of the *Lystrosaurus* Assemblage Zone (C. Northwood, unpub. Ph.D. thesis, La Trobe Univ. 1997). The discovery of *Lydekkerina huxleyi* in the Galilee Basin, to the west of the Arcadia Formation outcrops containing an Early Triassic fauna, suggests that a fauna more typical of the *Lystrosaurus* Assemblage Zone may have been present in uplands to the west of the Bowen Basin.

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References

- ARCHBOLD, N. W. & DICKENS, J. M. 1996. Permian (Chart 6). In *An Australian Phanerozoic timescale* (eds G. C. Young and J. R. Laurie), pp. 127–35. Melbourne: Oxford University Press.
- BALME, B. E. & FOSTER, C. B. 1996. Triassic (Chart 7). In *An Australian Phanerozoic timescale* (eds G. C. Young and J. R. Laurie), pp. 136–47. Melbourne: Oxford University Press.
- BANKS, M. R. & NAQVI, I. H. 1967. Some formations close to the Permo-Triassic boundary in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **101**, 17–31.
- BARTHOLOMAI, A. 1979. New lizard-like reptiles from the Early Triassic of Queensland. *Alcheringa* **3**, 225–34.
- BATTAIL, B. 1988. Biostratigraphie des formations Permo-Triassiques continentales à Vertébrés tétrapodes et biogéographie du Gondwana. *Annales de la Société Géologique du Nord* **107**, 37–44.
- BROMLEY, R. G. 1990. *Trace fossils: biology and taphonomy*. London: Unwin Hyman, 280 pp.
- BROOM, R. 1915. On the Triassic stegocephalians *Brachyops*, *Bothriceps* and *Lydekkerina* gen. nov. *Proceedings of the Zoological Society of London* **1915**, 363–8.
- BROOM, R. 1930. Notes on some labyrinthodonts in the Transvaal Museum. *Annals of the Transvaal Museum* **14**, 1–10.
- CANTRILL, D. J. & WEBB, J. A. 1998. Permineralised pleuromeid lycopsid remains from the Early Triassic Arcadia Formation, Queensland, Australia. *Review of Palaeobotany and Palynology* **102**, 189–211.
- CLACK, J. A. & HOLMES, R. 1988. The braincase of the antracosaur *Archeria crassidisca*, with comments on the interrelationships of primitive tetrapods. *Palaeontology* **31**, 85–107.
- COLBERT, E. H. & COSGRIFF, J. W. 1974. Labyrinthodont amphibians from Antarctica. *American Museum Novitates* **255**, 1–30.
- COSGRIFF, J. W. 1974. Lower Triassic Temnospondyli of Tasmania. *Geological Society of America, Special Paper* **149**, 1–131.
- DAMIANI, R. J. 2001. A systematic revision and phylogenetic analysis of Triassic mastodontosaurids (Temnospondyli: Stereospondyli). *Zoological Journal of the Linnean Society* **133**, 379–482.
- DAMIANI, R. J. 2004. Temnospondyls from the Beaufort Group (Karoo Basin) of South Africa and their biostratigraphy. *Gondwana Research* **7**, 165–73.
- DAMIANI, R. J., NEVELING, J. & HANCOX, P. J. 2001. First record of a mastodontosaurid (Temnospondyli, Stereospondyli) from the Early Triassic *Lystrosaurus* Assemblage Zone (Karoo Basin) of South Africa. *Neues*

- Jahrbuch für Geologie und Paläontologie, Abhandlungen* **221**, 133–44.
- EXON, N. F. 1970. *1:250 000 geological series – explanatory notes Tambo, Queensland*. Bureau of Mineral Resources, Geology and Geophysics, Canberra.
- EXON, N. F., GALLOWAY, M. C., CASEY, D. J. & KIRKEGAARD, A. G. 1972. Geology of the Tambo/Augathella area, Queensland. *Bureau of Mineral Resources, Geology and Geophysics, Canberra, Report* **143**, 1–105.
- FOSTER, C. B. 1982. Spore pollen assemblages of the Bowen Basin, Queensland (Australia): their relationship to the Permo–Triassic boundary. *Review of Palaeobotany and Palynology* **36**, 165–83.
- FOSTER, C. B. & JONES, P. J. 1994. Correlation between Australia and the type Tatarian, Russian Platform, evidence from palynology and Conchostracha: a discussion. *Permophiles* **24**, 36–43.
- FOSTER, C. B., LOGAN, G. A. & SUMMONS, R. E. 1998. The Permian–Triassic boundary in Australia: where is it and how is it expressed? *Proceedings of the Royal Society of Victoria* **110**, 247–66.
- GRECH, P. V. & DYSON, I. A. 1997. An integrated approach to the study of the Early Triassic Rewan Group, Bowen Basin. *APPEA Journal* **1997**, 194–204.
- GROENEWALD, G. H. & KITCHING, J. W. 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. In *Biostratigraphy of the Beaufort Group (Karoo Supergroup)* (ed. B. S. Rubidge), pp. 35–9. South African Committee for Stratigraphy Biostratigraphic Series 1.
- HANCOX, P. J. 2000. The continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie Teil I* **1998**, 1285–1324.
- HEWISON, R. H. 1996. The skull of *Deltacephalus whitei*, a lydekkerinid temnospondyl amphibian from the Lower Triassic of Madagascar. *Palaeontology* **39**, 305–21.
- HILLER, N. & STAVRAKIS, N. 1984. Permo–Triassic fluvial systems in the southeastern Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **34**, 1–21.
- HOWIE, A. A. 1972. A brachyopid labyrinthodont from the Lower Trias of Queensland. *Proceedings of the Linnean Society of New South Wales* **96**, 268–77.
- JEANNOT, A. M., DAMIANI, R. & RUBIDGE, B. S. In press. Cranial anatomy of the Early Triassic stereospondyl *Lydekkerina huxleyi* (Tetrapoda: Temnospondyli) and the taxonomy of South African lydekkerinids. *Journal of Vertebrate Paleontology*.
- JENSEN, A. R. 1975. Permo–Triassic stratigraphy and sedimentation in the Bowen Basin, Queensland. *Bureau of Mineral Resources, Geology and Geophysics, Canberra, Bulletin* **154**, 1–187.
- JUPP, R. & WARREN, A. A. 1986. The mandibles of the Triassic temnospondyl amphibians. *Alcheringa* **10**, 99–124.
- KASSAN, J. & FIELDING, C. R. 1996. Aspects of Triassic sedimentation in the Bowen Basin, Queensland. *Mesozoic Geology of the Eastern Australia Plate Conference, Brisbane, September 1996, Extended Abstracts* **43**, 292–302.
- LYDEKKER, R. 1889. Notes on the occurrence of a species of *Bothriceps* in the Karroo system of South Africa. *Annals and Magazine of Natural History* **6**, 475–6.
- KING, G. M. 1983. First mammal-like reptile from Australia. *Nature* **306**, 209.
- MCKELLAR, J. L. 1991. Palynostratigraphy. In *Stratigraphic drilling report – GSQ Muttaborra 1* (eds T. J. Brain, J. L. McKellar and D. C. Carmichael), pp. 15–20. Queensland Resource Industries Record 1991/25.
- MCLOUGHLIN, S., LINDSTRÖM, S. & DRINNAN, A. N. 1997. Gondwanan floristic and sedimentological trends during the Permian–Triassic transition: new evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica. *Antarctic Science* **9**, 281–98.
- MUNDIL, R., RENNIE, P. R., ZHOU, Z., METCALFE, I. & FOSTER, C. 2002. Timing of the Permian–Triassic transition: new U/Pb and 40Ar/39Ar radio-isotope ages from marine (S. China) and terrestrial (E. Australia) sections. *Geological Society of America, Denver Annual Meeting, Abstract* **222**, 13.
- NEVELING, J. 2004. Stratigraphic and sedimentological investigation of the contact between the *Lystrosaurus* and the *Cynognathus* assemblage zones (Beaufort Group; Karoo Supergroup). *Council for Geoscience Bulletin* **137**, 1–165.
- PARRINGTON, F. R. 1948. Labyrinthodonts from South Africa. *Proceedings of the Zoological Society of London* **118**, 426–45.
- PRICE, P. L. 1997. Permian to Jurassic palynostratigraphic nomenclature of the Bowen Basin and Surat Basins. In *The Surat and Bowen Basins, south-east Queensland* (ed. P. Green), pp. 137–78. Queensland Minerals and Energy Review Series, Queensland Department of Mines and Energy.
- ROMER, A. S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard College* **99**, 1–352.
- RETAILLACK, G., SMITH, R. M. H. & WARD, P. D. 2003. Vertebrate extinction across Permian–Triassic boundary in Karoo Basin, South Africa. *Geological Society of America Bulletin* **115**, 1133–52.
- SCHOCH, R. R. & MILNER, A. R. 2000. *Stereospondyli. Handbuch der Paläoherpetologie, Teil 3B*. Munich: Verlag Dr Friedrich Pfeil, 203 pp.
- SHISHKIN, M. A. 1980. The Luzocephalidae, a new Triassic labyrinthodont family. *Paleontological Journal* **14**, 88–100.
- 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 Transactions of the Royal Society of London Series B* **351**, 1635–59.
- 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.
- SWINTON, W. E. 1956. A neorhachitome amphibian from Madagascar. *Annals and Magazine of Natural History* **97**, 60–4.
- THULBORN, R. A. 1979. A proterosuchian thecodont from the Rewan Formation of Queensland. *Memoirs of the Queensland Museum* **19**, 331–55.
- THULBORN, R. A. 1983. A mammal-like reptile from Australia. *Nature* **303**, 330–1.
- THULBORN, R. A. 1986. Early Triassic tetrapod faunas of southeastern Gondwana. *Alcheringa* **10**, 297–313.
- TRIPATHI, C. 1969. Fossil labyrinthodonts from the Panchet Series of the Indian Gondwanas. *Palaeontologia Indica* **38**, 1–45.
- WARD, P. D., MONTGOMERY, D. R. & SMITH, R. M. H. 2000. Altered river morphology in South Africa

- related to the Permian–Triassic extinction. *Science* **289**, 1740–3.
- WARREN, A. A. 1980. *Parotosuchus* from the Early Triassic of Queensland and Western Australia. *Alcheringa* **4**, 25–36.
- WARREN, A. A. 1981. A horned member of the labyrinthodont superfamily Brachyopoidea from the Early Triassic of Queensland. *Alcheringa* **5**, 273–88.
- 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**, 303–27.
- WARREN, A. A. & HUTCHINSON, M. N. 1988. A new capitosaurid amphibian from the Early Triassic of Queensland, and the ontogeny of the capitosaur skull. *Palaeontology* **31**, 857–76.
- WATSON, D. M. S. 1919. The structure, evolution and origin of the amphibia. The “orders” Rhachitomi and Stereospondyli. *Philosophical Transactions of the Royal Society of London B* **209**, 1–71.
- WATSON, D. M. S. 1962. The evolution of the labyrinthodonts. *Philosophical Transactions of the Royal Society of London B* **245**, 219–65.
- YATES, A. M. 1999. The Lapillopsidae: a new family of small temnospondyls from the Early Triassic of Australia. *Journal of Vertebrate Paleontology* **19**, 302–20.
- ZITTEL, K. A. VON. 1887–1890. *Handbuch der Paläontologie. Abteilung 1. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. Munich and Leipzig: Oldenbourg, 900 pp.